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FISH AND WILDLIFE SERVICE • Arnie J. Suomela, *Commissioner*

NATURAL HISTORY OF THE SANDBAR SHARK *EULAMIA MILBERTI*

By STEWART SPRINGER

March 3, 1849

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ABSTRACT

Populations of sandbar sharks of the eastern and western parts of the Atlantic Ocean are defined and general problems of nomenclature, the ecology of large carcharhinid sharks, and field recognition of sandbar sharks are discussed.

A more-detailed account of observations on *Eulamia milberti*, restricted to the population of the western North Atlantic, is given, outlining distribution of adults and young, migrations, development, and behavior, based on observations from the commercial shark fishery which operated from centers in the Southeastern States from 1935 to 1950 and supplemented by data from research vessels operating after 1950.

Comparisons with other species in the area, lists of large species of sharks taken at certain times off Salerno, Florida; Bimini, Bahamas; the mouth of the Mississippi River, Louisiana; and the Caribbean coast of Nicaragua-Costa Rica, as well as discussions of interspecies competition, are included.

NATURAL HISTORY OF THE SANDBAR SHARK, *EULAMIA MILBERTI*

By Stewart Springer, *Fishery Methods and Equipment Specialist*
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This account of the sandbar shark, *Eulamia milberti* (Müller and Henle), is an attempt to bring together all the significant information on one kind of common and moderately large shark. Sharks have been studied because they are occasionally dangerous to man, often a nuisance to fishermen and, in the past at least, have been valuable as a source for food, leather, vitamin A, fish meal, and some specialty products. A rather comprehensive body of knowledge exists about some of the smaller species, such as the comparatively valuable soupfin shark of the coast of North America (Ripley, 1946) and the school shark of Australia (Olsen, 1954), both species of *Galeorhinus*, and the common spiny dogfish, *Squalus* (Ford, 1921; Hickling, 1930; Templeman, 1944). Information on the natural history of the larger species is fragmentary. This is to be expected, because large species not only are difficult to catch and handle, but also are far-ranging and require observation over a wide geographical area.

The sharks, together with their relatives, the skates, rays, and chimaeroids, form a class of vertebrates that is sharply set off from the classes which contain the fishes, amphibians, reptiles, birds, and mammals. The sharks and other members of the class Chondrichthyes have cartilaginous skeletons, and while elements of the shark skeleton may become calcified, no true bone is formed. This is the basis for the definition that is generally used to distinguish the Chondrichthyes from the higher vertebrates. But there are other differences in the chemistry and physiology that are very likely of great importance but are little understood. The evolutionary connections of the modern sharks and their allies with other modern vertebrates are obscure and of great antiquity.

Sharks occupy a place in nature at the top of the food chain. As predators they compete with man, but it is by no means established that their predatory activities are always harmful. They are a nuisance or are harmful to fishermen chiefly because of the damage they do to nets or to fish that have been caught on setlines. In some localities, in England and Australia, for example, sharks are utilized and are consequently of some value. In the United States, landings at present are of no great importance.

Sharks may be dangerous to man through attacks on swimmers and survivors of marine disasters, but *Eulamia milberti* is not a species implicated in well-documented records of attacks. There may be several reasons for this. *E. milberti* ordinarily stays away from beaches and does not often feed at the surface. It usually seeks small prey. During the summer, when the female sandbar sharks come inshore near the heavily populated centers from New York southward along the Atlantic coast to give birth to their young, it is not their habit to seek food. The large males do not come inshore. So the sandbar shark, while large enough to be dangerous and perhaps the most common of the larger sharks in shore waters southward from New York, is isolated by its habits from encounters with man. Nevertheless, the sandbar shark is potentially dangerous to man and might become a more serious danger with minor shifts in the environmental situation.

The most annoying aspect of my work with sharks, prior to the publication in 1948 of the first volume of Fishes of the Western North Atlantic on sharks by Dr. Henry B. Bigelow and William C. Schroeder, was that many western Atlantic sharks could not be identified with confidence because of a scattered literature of varying quality. It is appropriate that I acknowledge the importance of this excellent general work to me, because without it and without the encourage-

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Note.—Approved for publication, October 27, 1958. Fishery Bulletin 178.

ment of its authors, I would not have attempted preparation of this report. Dr. Richard H. Backus of the Woods Hole Oceanographic Institution, Dr. Giles W. Mead of the U.S. Fish and Wildlife Service, and Dr. Leonard P. Schultz of the U.S. National Museum made many helpful suggestions during the preparation of this report. Captain B. W. Winkler was especially helpful in keeping fishing logs and measurements of about 1,300 large sharks he took off the Bahama Banks and off Nicaragua. Records obtained while I was employed by the Shark Industries Division of the Borden Company and while I was aboard the exploratory fishing vessel *Oregon* of the Fish and Wildlife Service comprise the basic data used here. Special assistance was given me also by the Lerner Marine Laboratory of the American Museum of Natural History, by permitting 2 months of field study at Bimini, Bahamas, in the summer of 1948. In all my work with sharks, I have been given the most generous help by my associates in commercial shark fishing and aboard exploratory fishing vessels.

NOMENCLATURE

This report is not intended to settle problems of nomenclature and taxonomy, but to be useful it is necessary to name the sharks under discussion and to define the names used. My choice of a name for the sandbar shark is *Eulamia milberti* (Müller and Henle) 1841. Use of *Eulamia* follows my partial revision of the carcharhinids (Springer, 1950). For the specific name *milberti* I follow Bigelow and Schroeder (1948) who note that, if it is finally proved that the Mediterranean form is identical with the American, the name *plumbeus* Nardo 1827, must be used for the combined species in place of *milberti*.

I disagree, however, with Fowler (1936), with the preceding statement by Bigelow and Schroeder, and with Tortonese (1951, 1956) that Nardo's description is valid. The description by Nardo would apply to almost any carcharhinid and the specific mention of the rounded snout[1] would apply better to some other carcharhinids than to the sandbar shark. Because there is no type and because Nardo's description would apply to almost any carcharhinid if applied liberally but to none if applied strictly, I regard *Squalus plumbeus* as a *nomen nudem*.

I am also unable to accept Nardo's description as specifically applicable to the sandbar shark based on the argument that the sandbar shark is the most common large carcharhinid of the Adriatic.

A most extraordinary snarl has developed over the years in the determination of the scientific name to be applied to the sandbar shark. The origin of this complication probably lies in the peculiarities of the distribution of species of carcharhinid sharks along the Atlantic coast of the United States. Mistakes in identification of specimens have been frequent, probably because the descriptive accounts of the early authors were very brief and did not select truly diagnostic features for emphasis. Systematists had too few specimens and too little data on distribution to note that segregation of the sexes and segregation of the adults and young characterized these sharks at some seasons.

In the latitudes from New York to Chesapeake Bay at depths within easy reach of collectors or fishermen, two common large carcharhinid sharks occur, the sandbar shark, *E. milberti* (Müller and Henle), and the bull shark, *Carcharhinus leucas* (Müller and Henle). The sandbar shark is represented in this area by adult females and by the young of both sexes, but rarely by adult males in the observable elements of the population. The bull shark is represented usually by adult males, but females and young are also present sporadically.[2]

The ranges of the sandbar shark and the bull shark will be discussed later as well as the apparent competition between these species. An effect of the occurrence of the two species together, however, has been to foster confusion in the nomenclature. There appears to have been a tacit assumption by some naturalists that sexual dimorphism accounted for differences in sandbar sharks and bull sharks despite recognition of the existence of both species.

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[1] The total description and diagnosis of *Squalus plumbeus* by Nardo, 1827, p. 35, is as follows: "Speciei secundae convenit exacte *Squal. Glaucus.* Bloc. si color exciperetur et forma rostri quae in exemplari nostro rotunda est."

[2] Large male *Carcharhinus leucas* were reported from the Chesapeake Bay area by Schwartz (1958); one was taken from the Patuxent River in 1957 and another at Flag Pond in the summer of 1958. This is apparently the first published report of the species from Chesapeake Bay. Specimens of large sharks came to the attention of Edgar H. Hollis, of the Maryland Department of Tidewater Fisheries in 1957, because Chesapeake fishermen regarded them as rarities. Photographs of the specimens sent me by Mr. Hollis were sufficient to permit identification as *C. leucas*. Nichols (1918) and Nichols and Breder (1927) reported *C. leucas* from the south shore of Long Island, noting that these specimens were large males. Attention is called to this parenthetically because the appearance of adult males at the periphery or in the cooler parts of ranges of carcharhinid sharks is frequent.

Superficially, the sandbar shark and the bull shark resemble one another but, as will be shown later, sandbar sharks can easily and positively be separated from bull sharks on the basis of several anatomical characteristics. Identification of specimens from the Middle Atlantic States, particularly the Atlantic coast from Cape Cod to Chesapeake Bay, presents an added difficulty because of the several very similar offshore species which may be caught occasionally, but probably rarely in inshore waters: *Eulamia obscura* (Le Sueur), *E. falciformis* (Müller and Henle), *E. floridana* (Bigelow, Schroeder, and Springer), and *E. altima* Springer. Recent unpublished records of the occurrence of *E. milberti* young and of the occurrence of *Carcharhinus leucas* adults are rather numerous, and following publication of the first volume of Fishes of the Western North Atlantic (Bigelow and Schroeder, 1948) there appears to be little confusion of the two species.

Belaboring the point that descriptive accounts of carcharhinids must be detailed and selective to have any meaning seems necessary to affect the intrenched misconceptions about *E. milberti* that can be derived from the literature. Fowler's (1936) description of *E. plumbeus* (*plumbeus*=*milberti*), which was based on American Middle States examples, although in a report on West African marine fishes, is not unique in confusing *E. milberti* with another species,[3] but it is detailed enough to be especially vulnerable to criticism. More elements of his description fit the bull shark, *Carcharhinus leucas*, than *E. milberti*, but additional confusion is introduced by the probability that juvenile and adult characteristics of both species are mixed. There is no selection of diagnostically useful characteristics for emphasis. The result is a plausible literary synthesis that is a hazard to one attempting to fit a real shark to a position in zoological classification.

POPULATIONS OF *EULAMIA MILBERTI*

Sandbar sharks, *Eulamia milberti*, occur in portions of the temperate and tropical Atlantic, the Caribbean, the Gulf of Mexico, and the Mediterranean. Our data in this study primarily cover the population inhabiting the western North Atlantic, the Gulf of Mexico, and the eastern Caribbean. Later, the normal movements and distribution of this population will be discussed. We need first to consider the relationships of the various populations. In addition to the population of the western North Atlantic two others may be roughly defined. One occurs along the coast of South America from Trinidad eastward and southward. The other is found along the west coast of Africa and is presumed to be continuous with the stock entering the Mediterranean.

The population occurring on the coast of South America appears to be a minor one. The species has been reported and figured by Ribiero (1923) from the coast of Brazil.

While engaged in commercial shark fishing in April and May 1949, I made shipboard examinations (Springer, 1949) of a series of sandbar sharks from the north and east coasts of Trinidad and identified them in error as *E. plumbeus*. I now believe that differences between the Trinidad specimens and typical *milberti* from the Atlantic coast of the United States are insufficient to warrant recognition of separate species, and that the conservative course, pending accumulation of new data, is to look upon the various Atlantic sandbar sharks as representing a single species. At the Trinidad locations, adult males and females as well as young of all sizes from 4 feet upward were taken on single setlines. Although commercial shark fishing was carried on throughout 1949 from the coast of French Guiana westward to the Gulf of Venezuela, sandbar sharks were reported only from the north and east coasts of Trinidad and chiefly from depths of 5 to 20 fathoms near Galera Point.

There are no records of sandbar sharks from the West Indies north of Trinidad except from the north coast of Cuba and from the western part of the Bahama Banks. This is not, of course, conclusive evidence of their absence from a region so poorly known ichthyologically as the West Indies. Nevertheless, all of the evidence points to a discontinuous distribution with no regular contact between the population known from Cape Cod to Costa Rica and the South American population known from Trinidad and the east coast of South America south of the Amazon.

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[3] Garman's illustration of *Carcharhinus platyodon* (1913, pl. 3, figs. 4 and 6) appears to be very well drawn from a specimen of *Eulamia milberti*. Bigelow and Schroeder (1948) note that Garman's illustration is mislabeled. The accompanying illustration of the teeth in Garman's plate 3, figure 5, appears to have been drawn from the teeth of *platyodon*. *Carcharhinus platyodon* (Poey) is a synonym of *C. leucas* (Müller and Henle).

In connection with possible future work with the sandbar sharks, it should be noted that the *E. milberti* from Trinidad were taken in eddies of the very strong, westerly current flowing between Trinidad and Tobago; and that recruitment for this stock could take place in part by transport by the Equatorial Current of the growing young to Trinidad from shore waters of the African coast.

The stock of *Eulamia milberti* in the eastern Atlantic is known from scattered records from the Mediterranean and the west coast of North Africa as summarized by Tortonese (1956). These records cover a long period of time and although critically reviewed by Tortonese and unquestionably accurate, they give little basis for an estimate of the abundance of the sandbar shark in relation to the abundance of other large species of the area. For our purposes here, that is, to estimate the relative importance and abundance in comparison with other large sharks of the area, reports by Cadenat (1950, 1957) on *E. milberti* and other species from the coast of Senegal are quite informative. Cadenat has been able to make observations on fresh material from a fishery taking relatively large numbers of the larger species of sharks. His reports suggest that the stock of *E. milberti* off northwest Africa is a strong one.

The list of species of large sharks reported by Cadenat is quite similar to lists of large sharks from the southeastern coast of the United States. The endemic species of both areas are the smaller sharks.

Precisely the same factors of prevailing wind and surface currents that make the southern crossing from the North African coast to Trinidad easier for man when it is from east to west may be expected to operate for sharks. Similarly, for a more northerly crossing, the one from west to east is more easily followed. The postulate that such contacts as exist between the stocks of the western Atlantic and the stock of the eastern Atlantic result from exchanges following this general clockwise circulation is a reasonable one. No actual evidence of regular contacts between the three stocks exists, however, and there is substantial reason for the belief that movements of individual sharks from one stock to another are relatively infrequent occurrences.

Knowledge of the distribution of large sharks in oceanic situations at considerable distance from land was extremely meager until very recently when data from oceanographic vessels and exploratory fishing vessels became available. The most comprehensive study covers sharks of the Central Pacific (Strasburg, 1958) in which data showing patterns of distribution of some of the larger species is given. Before the appearance of that study and of a less comprehensive account of Atlantic pelagic sharks (Backus et al., 1956), questions of shark distribution seaward of the continental shelves were unanswerable.

Now, while it is known that neritic species of large sharks are capable of moving over great distances of open ocean, there is increasing evidence that they rarely do.

ECOLOGICAL AND SYSTEMATIC RELATIONSHIPS OF THE GENUS *EULAMIA*

The genus *Eulamia* may be divided into two groups on the basis of the structure and arrangement of the dermal denticles. The group to which *E. milberti* belongs is characterized by nonimbricate denticles as contrasted with the other group which has denticles with overlapping edges or points. The *milberti* group includes comparatively few species. Probably *Eulamia dussumieri* (Müller and Henle) and *E. japonicus* (Schlegel) of the western Pacific belong here. In the Atlantic, the group is represented by a deep-water species, *Eulamia altima* Springer, which is quite different from *milberti*, not only in its morphology but in its habitat. Aside from *E. altima*, the only Atlantic representative of the genus *Eulamia* (or any carcharhinid genus) with widely spaced, nonimbricate denticles is *Eulamia milberti*, the sandbar shark.

E. milberti has the shoalest range and occupies the most inshore habitat of any of the 5 or 6 species of *Eulamia* of the Atlantic coast of North

America. Although *milberti* may be in competition with other species of *Eulamia* for food in some parts of its range, it does not compete with other species of *Eulamia* for nursery grounds.

Of the other carcharhinids of the northwestern Atlantic, the genera *Prionace* and *Pterolamiops* are pelagic surface dwellers; *Hypoprion* is confined to waters generally deeper than 100 fathoms near shelves or banks; *Negaprion*, *Apriondon*, *Scoliodon*, and *Carcharhinus* are shallow water sharks that spend at least some part of their lives in shallow lagoons, river mouths, or estuaries, and venture into deeper water rarely except for transitory movements; the species of *Eulamia* are sharks of the continental shelves, oceanic banks, and island terraces, although some species extend their ranges well inshore and also for considerable distances beyond the limits of the Continental Shelf. The only other western North Atlantic carcharhinid genus, *Galeocerdo*, is represented by a single species in subtropical and tropical waters out to depths of at least 200 fathoms. It does not exhibit the specialized schooling habits of the other carcharhinids, shows no strong migratory tendencies, and is less restricted in habitat choice than the others. There seems to be a tendency to greater variation in the number of young produced as well as a greater number per litter in *Galeocerdo* and *Prionance* and possibly also in *Pterolamiops* than in other northwestern Atlantic carcharhinids. Insofar as is known, there are no very important differences in the general outlines of the life history patterns of *Negaprion*, *Aprionodon*, *Scoliodon*, *Carcharhinus*, and *Eulamia*, although there appear to be many differences in detail.

Barriers which may restrict the movements of the larger sharks including *Eulamia milberti* are not readily apparent. Occasional captures of sharks outside areas of normal concentration of the species prove that they can and do wander. The remarkable thing is that large sharks tend to remain within definable habitats and geographical ranges.

Since species of *Eulamia* are, in general, less dependent on land masses than *Carcharhinus* and extend their activities regularly to surface waters of the open ocean beyond the Continental Shelf, it would not be surprising to find that some species have a very wide distribution in temperate and tropical seas. *Eulamia floridana* (Bigelow, Schroeder, and Springer) may be an example of such a distribution (see Strasburg, 1958). Those species of *Eulamia*, such as *milberti*, which are tied to shallow-water habitats are presumably subject to a greater degree of isolation.

SPECIMENS EXAMINED

Specimens, records, and field observations for this report have been assembled over a period of about 25 years during which time I have examined several thousand sandbar sharks. Available records of the commercial shark fishery cover more than 100,000 adult *Eulamia milberti*. About half of these sharks were measured at the point of landing. Earlier records of the stations included specimens of *Eulamia altima* and *Eulamia floridana* under the heading sandbar sharks. Since I visited most of the stations frequently, and during part of the period between 1935 and 1950 supervised recording procedures, I saw relatively large numbers of sandbar sharks. Specimens which appeared unusual to station employees were retained when practicable for my inspection. Most of my observations were made along the coasts of southern Florida. Adequate numbers of specimens for some purposes have been examined from the eastern and northern parts of the Gulf of Mexico, the Atlantic coast of the United States south of Cape Cod, and from the Caribbean coast of Nicaragua and Costa Rica. The available material in several museum collections in the United States was studied, but this consisted chiefly of preserved embryos or very young sharks and dried jaws.

The collection of data in the shark fishery suffered from interruptions and was assembled to aid an industrial operation rather than for a biological study. The difficulty in handling specimens, averaging nearly 7 feet in length as adults with an average weight of about 135 pounds, has made it necessary to select different series or samples for different objectives: one sample for length-weight relations; another for tooth counts, and so on.

I was unable to find spirit-preserved specimens of eastern Atlantic or Mediterranean origin referable to either *E. plumbeus* or *E. milberti* during a hasty examination of catalogs and specimens at the Museum d'Historie Naturelle in Paris or in the British Museum of Natural History, although specimens from the western Atlantic were present. Tortonese noted (1938) that there are two specimens in the Musee di Trieste collected in 1869 and 1871 and, after examination of specimens labeled *milberti* from the western Atlantic in the Museum at Paris and the British Museum, he indicated (in 1951) that he regards *milberti* as a synonym of *plumbeus*.

FIELD RECOGNITION

Eulamia milberti is commonplace in appearance. It has neither unusual color markings nor spectacular structural features. The length of the shark at maturity, 7 feet, makes the species too large for the biological collector and too small to interest the journalist. It is necessary to search for distinguishing features (fig. 1). The opportunity for comparison of series under ordinary circumstances is negligible, and almost all identifications of the larger sharks are necessarily made in the field. The suggestion that many of the presently recognized species of carcharhinid sharks are not in fact separable from one another but should be regarded as unidentifiable parts of a species complex has been advanced in speculative conversation by some of my friends who are ichthyologists. This view may easily develop from unsatisfactory attempts to make identifications with methods which are quite adequate and successful in application to teleosts but fall short when applied to sharks, and particularly to carcharhinid sharks. *E. milberti*, in waters off the United States, is readily defined and problems concerning it are not complicated by the existence of geographic or environmental races or subspecies, insofar as the available evidence shows. This is apparently not true of some of the other carcharhinids where separate populations may be defined on the basis of morphological differences shown in the analysis of adequate series from different areas.

The keys and descriptions given by Bigelow and Schroeder (1948) are adequate for the identification of the carcharhinid sharks of the western North Atlantic excepting *Eulamia altima*, which was described (Springer, 1950) after publication of this work. Nevertheless, identifications need to be made carefully because of the general structural similarity of the species which look alike on superficial examination. Sharks of the genus *Eulamia* in the *falciformis-springeri* group are

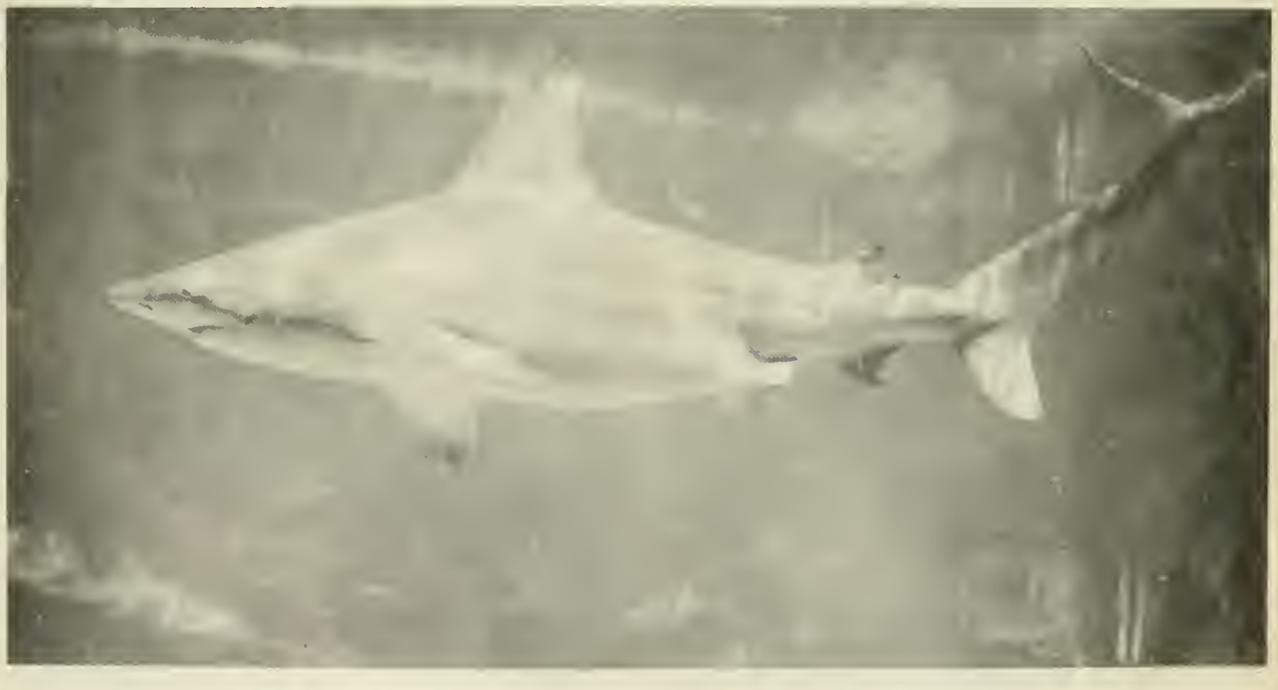

FIGURE 1.—*Eulamia milberti* in an exhibition tank. The high, triangular first dorsal fin, nonfalcate pectoral fins, and relatively high second dorsal and anal fins, nearly equal to one another in area, are characteristic of the species. (Photograph courtesy of Marine Studios, Marineland, St. Augustine, Fla.)

not well known and possibly are incompletely defined. Minor differences between Atlantic and Gulf of Mexico populations of *E. obscura* need further study. There is no difficulty, however, in distinguishing *E. milberti* from these species or from other species of sharks ordinarily found within its geographical range.

The importance of determining the presence or absence of a middorsal ridge (a low ridge in the skin extending for all or a part of the distance between the first and second dorsal fins) for the identification of carcharhinid sharks cannot be overemphasized. This minor structural feature is certainly nonadaptive and its usefulness as an indicator of probable relationships should be great (see Springer, 1950: p. 1, and Backus, Springer, and Arnold, 1956: p. 180, for discussion). The first mention of this characteristic in published work was by Nichols and Breder (1927), but correct identifications of the common large ground sharks of the east coast of the United States were made by Nichols and by Radcliffe independently before 1916.

In one of the more valuable papers on sharks, Radcliffe (1916) made the first general use of the structure of the dermal denticles to show differences in western North Atlantic carcharhinid species; and his illustrations show clearly the distinctive denticle type and arrangement which sets *E. milberti* off from other carcharhinids within its range, except for the newly described *E. altima*. Both *E. milberti* and *E. altima* differ from all other North American carcharhinid sharks in having nonimbricate denticles without strongly projecting points; however, the denticles of *E. altima* are much smaller than those of *E. milberti.*

Commercial shark fishermen at Salerno and Key West, Fla., recognized *altima* as distinct from the sandbar shark and called it the bignose shark or Knopp's shark before it received a scientific name. The diagnosis given with the original description of *E. altima* (Springer, 1950) should be adequate for the determination of specimens of all sizes. All of the known examples of *E. altima* have been taken at depths of 50 to 150 fathoms off Salerno, Florida, in the Straits of Florida, in the northeastern Gulf of Mexico, and n the Dragon's Mouth between Trinidad and Venezuela. Its vertical range overlaps that of the shallower water *E. milberti* in the Straits of Florida area and extends well into the nighttime range of the night shark, *Hypoprion signatus* Poey. The geographical range of *E. altima* may be quite extensive, but it is unknown because comparatively little fishing has been carried out at the depths where this species might be expected to occur. Such fishing as has been done in midwater and just beyond the edges of the Continental Shelf by commercial shark fishermen indicates that the species is relatively common.

Probably many more *E. altima* would have been taken by the commercial fishery were it not for the fact that in the Florida-Caribbean region the liver oil of *altima* is characteristically lower in vitamin-A content than is that of any of the other species of *Eulamia* or of *Hypoprion* in that area.

In a large measure, the confusion in the nomenclature of the larger American carcharhinids that existed before the publication of the 1948 work by Bigelow and Schroeder would undoubtedly have been avoided if descriptive literature had included information on the presence or absence of the middorsal ridge. A fine replica of a shark, which in the light of the better descriptions now available can easily be identified as *Carcharhinus leucas* (Müller and Henle), a species without a middorsal ridge, is shown in an illustration in an informative article (Rockwell, 1916: p. 161) under the caption *Carcharhinus obscurus* (*Eulamia obscura*), a species with a middorsal ridge. Determination of the presence or absence of the ridge is sometimes difficult, particularly for museum specimens or for specimens that have been exposed to the sun for a long period. Although identifications can be made without reference to the ridge, they are likely to be difficult and use of all of the available differentiating characteristics is desirable.

The confusion of the sandbar shark with the bull shark extends to the Pacific. References have frequently been made to the sandbar shark, *Eulamia milberti*, as occurring on the Pacific coast of Panama. There is no evidence of this and the species probably is not found there. Garman's (1913) synonymy of *milberti* included *Eulamia nicaraguensis* Gill and Bransford, the fresh-water bull shark. The two bull sharks, *nicaraguensis* and *leucas* are so similar to one another that their separation is doubtful. There is a Pacific species so similar to *nicaraguensis* and *leucas* that commercial shark fishermen who fished on both coasts claimed they were unable to distinguish one from the other except by area of capture. I do not know the scientific name for the form if it has a name, but whatever the species, it is like *nicaraguensis* or *leucas* and not like *milberti.* Meek and Hildebrand seemingly had difficulties with this one in Fishes of Panama (1923), wherein they discuss a Pacific species *Carcharhinus azureus* (Gilbert and Starks) as a synonym of *milberti.* But Meek and Hildebrand did not see a specimen from the area which they themselves could identify as *milberti* and the significant sentence in their treatment states—

> We certainly must regard the present arrangement as tentative only, for more specimens must be compared before the true affinities of the specimens from the opposite coasts can be established.

A paper by Rosenblatt and Baldwin (1958) on some of the carcharhinids of the eastern Pacific presents for the first time information on the presence or absence of the middorsal ridge in Pacific species. This is an important contribution and includes more comprehensive descriptions than have hitherto been available for sharks of the eastern tropical Pacific. These authors find the separation of *Eulamia* from *Carcharhinus* unacceptable for Pacific species. In support of this an unfortunate choice of illustrative argument is used. They say *C. altima*, for example, has a definite dermal ridge but teeth which are as narrow as those of any member of the smooth-backed group (Springer, 1950). This is an error. The teeth of *altima* in the upper jaw are similar in general shape to the teeth of the other species of *Eulamia.* These authors logically call attention to the ill-assorted group left in the genus *Carcharhinus* by my 1950 revision, mentioning *leucas* and *velox* as examples. I am in complete agreement with this but find no cogent argument for the elimination of *Eulamia*, since the species of *Eulamia* as restricted are remarkably similar to one another in all of their morphological features. The sharks allied to the genus *Carcharhinus* are far too widespread and numerous and there is far too little known about them for an adequate study of the entire group. Additional revisions of the group are needed.

Differences between adults of *E. altima* and *milberti* are quite apparent in field examination when the two are seen side by side. The snout of *altima* is longer and notably thicker dorsoventrally. Furthermore, the first dorsal fin in *E. altima* looks quite different because it is not quite so far forward as in *E. milberti* and is neither so erect nor so high. The high and erect dorsal fin of *E. milberti* in a forward position (fig. 2) is a reliable and adequate character for field recognition of adults in the water, if the size of the shark is taken into consideration.

Gill (1862) based his classification of the carcharhinid sharks almost entirely on the structure of the teeth. His arrangement of genera was not satisfactory and it is apparent that short descriptions of shark teeth are inadequate and lead to confusion even though the number and form of the teeth show comparatively little variation within species and are of considerable diagnostic value. The persistence of essentially similar shape and structure in the successively larger teeth appearing in some carcharhinid sharks as they grow has been fairly well established by observation. In *E. milberti*, at least, this appears to be true, although this is neither universal among sharks nor adequately demonstrated for many species.

To obtain some verification of the extent of variation in the number of tooth rows in carcharhinid sharks, I took advantage of a situation requiring the preparation of several hundred clean, dry shark jaws for a commercial order. I carefully identified the sharks and tagged the jaws of a series of 110 *E. milberti* together with all other sharks appearing at the same time on the dock at Salerno, Fla. All of the *milberti* and most of the other sharks were adults; sex was not noted. After the jaws were cleaned I counted and recorded the number of tooth rows (table 1). To the extent that this sample represents the population of *milberti*, the counts of rows of teeth indicate that variation is small in that species.

The shape and the relative position of the fins in carcharhinid sharks are reasonably useful characteristics for identification. Small differences in the size of fins or even in their positions, however, are of comparatively little value because of differential growth and the diverse trends this

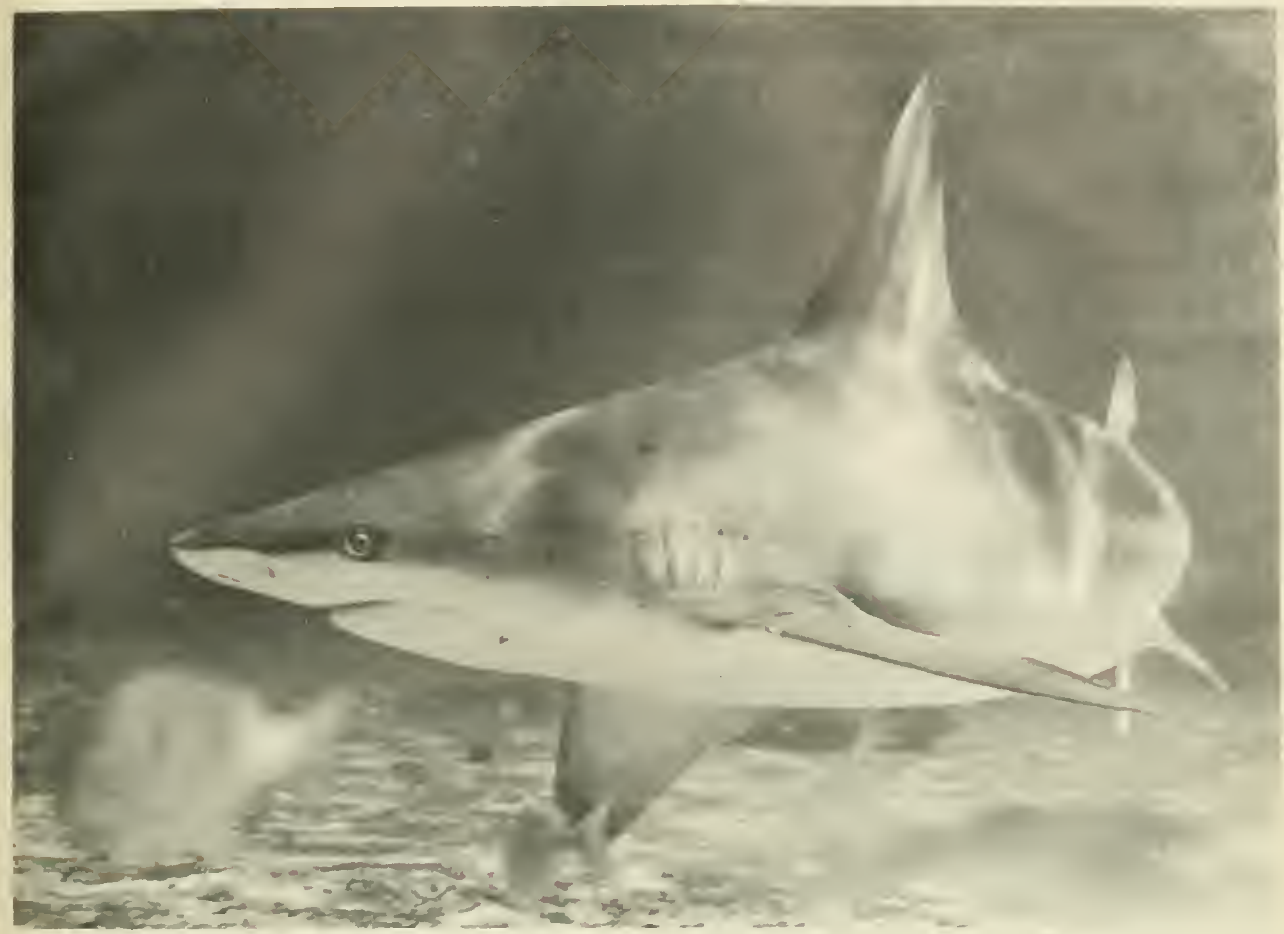

FIGURE 2.—*Eulamia milberti* turning in front of the camera at Marineland, Fla. Note that the pectoral fins are quite broad at their bases, relatively pointed and not strongly concave on their trailing edges. With the exception of the caudal fin, all fins function as rudders or stabilizers and cannot be used independently for locomotion The pectorals provide lift to offset the lift of the asymmetrical caudal since without a forward lift the shark would tend to somersault. The large stiff fins in forward positions reduce the ability of this species to roll and twist but may be expected to increase the precision of its forward swoops at creatures on the sea bottom. (Photograph courtesy of Marine Studios, Marineland, Fla.)

growth may take in different species. Data to show adequately the differential growth in carcharhinids are lacking. But one example will suffice to show how unreliable proportional measurements can be for comparisons between species in which specimens of different sizes and ages are involved, and in which the growth patterns of the species being compared are unknown. In three examples of young *E. milberti*, 685, 680, and 635 mm. long, from the vicinity of Woods Hole, Mass., the lengths of pectoral fins (measured on their outer margins or leading edges) are 16.2, 15.9, and 15.0 percent of the total length of the sharks. In three adult *milberti* from off Englewood, Fla., 2,210, 2,070, and 2,240 mm. long, the pectoral fin lengths are 21.3, 21.5, and 21.0 percent of the total length. Let us compare these proportions with measurements of pectoral fin lengths of the whitetip shark, *Pterolamiops longimanus* (Poey). A late-embryo whitetip 530 mm. long, taken 135 miles off New Smyrna, Fla., has a pectoral fin length 22.6 percent of the total length; a young whitetip 1,020 mm. long, taken off Tampico, Mexico, has a pectoral fin 25.5 percent of the total length; and an adult whitetip, 2,310 mm. long, from the central Caribbean, has a pectoral fin 22.0 percent of the total length. The figures indicate a proportionately longer

TABLE 1.—*Tooth-row counts in carcharhinid sharks taken off Salerno, Fla., summer of 1947*

Species	Number of specimens baving toothrow counts [1] of—																
	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37
Eulamia milberti (110 specimens):																	
Upper jaw	----	----	----	----	----	----	----	3	37	55	11	4	----	----	----	----	----
Lower jaw	----	----	----	----	----	----	12	20	44	30	3	1	----	----	----	----	----
E. floridana (48 specimens):																	
Upper jaw	----	----	----	----	----	----	----	----	----	----	1	29	11	3	1	3	----
Lower jaw	----	----	----	----	----	----	----	----	----	1	6	13	23	4	1	----	----
E. obscura (39 specimens):																	
Upper jaw	----	----	----	----	----	----	----	----	3	15	12	7	2	----	----	----	----
Lower jaw	----	----	----	----	----	----	1	3	15	10	8	1	1	----	----	----	----
Carcharhinus leucas (24 specimens):																	
Upper jaw	----	----	----	----	2	5	15	1	1	----	----	----	----	----	----	----	----
Lower	----	----	----	----	18	3	3	----	----	----	----	----	----	----	----	----	----
C. limbatus (31 specimens):																	
Upper jaw	----	----	----	----	----	----	----	----	1	0	4	14	11	0	1	----	----
Lower jaw	----	----	----	----	----	----	----	----	1	25	5	----	----	----	----	----	----
C. maculipinnis (13 specimens):																	
Upper jaw	----	----	----	----	----	----	----	----	----	----	----	1	1	2	4	3	2
Lower jaw	----	----	----	----	----	----	----	----	----	----	2	1	9	1	----	----	----
Galeocerda cuvier (21 specimens):																	
Upper jaw	4	3	12	2	----	----	----	----	----	----	----	----	----	----	----	----	----
Lower jaw	1	2	13	2	3	----	----	----	----	----	----	----	----	----	----	----	----
Negaprian brevirostris (8 specimens):																	
Upper jaw	----	----	----	----	----	----	----	----	----	1	1	6	----	----	----	----	----
Lower jaw	----	----	----	----	----	----	----	----	5	1	2	----	----	----	----	----	----

[1] All counts made from cleaned jaws from which all membranous sheathing had been removed to permit accurate counts whether or not teeth of the functional row were missing.

pectoral fin in adults than in young for *E. milberti*, but an entirely different condition in *P. longimanus*.

The sandbar sharks available to me were remarkably uniform in general appearance and in those features that I could measure, count, or compare. In an attempt to learn something from morphometrics, a considerable number of *milberti* and other species were measured carefully and in detail. However, the principal value that I derived from this excessively laborious task was in the deliberate examination of specimens enforced by measurement of detail and in the notes made to accompany the measurements. The exercise served also to impress upon me the difficulties attending attempts to get adequate series to show growth patterns among some of the species of large sharks which are not only migratory but probably short lived.

A characteristic of great importance for field recognition of specimens of carcharhinid sharks is the total length of the specimen considered in connection with its sex and maturity (fig. 3). The mammalogists and ornithologists have long considered total length important in identification because mammals and birds have determinate growth patterns. As will be shown later, *E. milberti* has growth characteristics which result in adults of predictable size. Furthermore, the size range of adults within the known segments of the population falls within limits which are narrow enough to facilitate field identification by process of elimination. Thus, an adult *Eulamia* more than 92 inches in total length is probably not *milberti*, and adult males less than 70 inches or adult females less than 72 inches in total length are unknown.

DISTRIBUTION OF *EULAMIA MILBERTI*

General nature of distribution

The distribution of *Eulamia milberti* is difficult to treat adequately because, even though further discussions will be limited to the population of the western North Atlantic, the distribution patterns are extremely complex. The adults segregate by sex and to some degree have different vertical ranges. The nursery areas occupied by the very young sharks are free of adults except when the females come inshore to give birth to their young.

The migratory patterns of young and adults differ greatly. Finally there is a well-defined principal range occupied by at least nine-tenths of the western North Atlantic population and an accessory range of uncertain importance. It is quite possible that the population occupying the accessory range is not self-sustaining and exists only because there is continuous but quite acci-

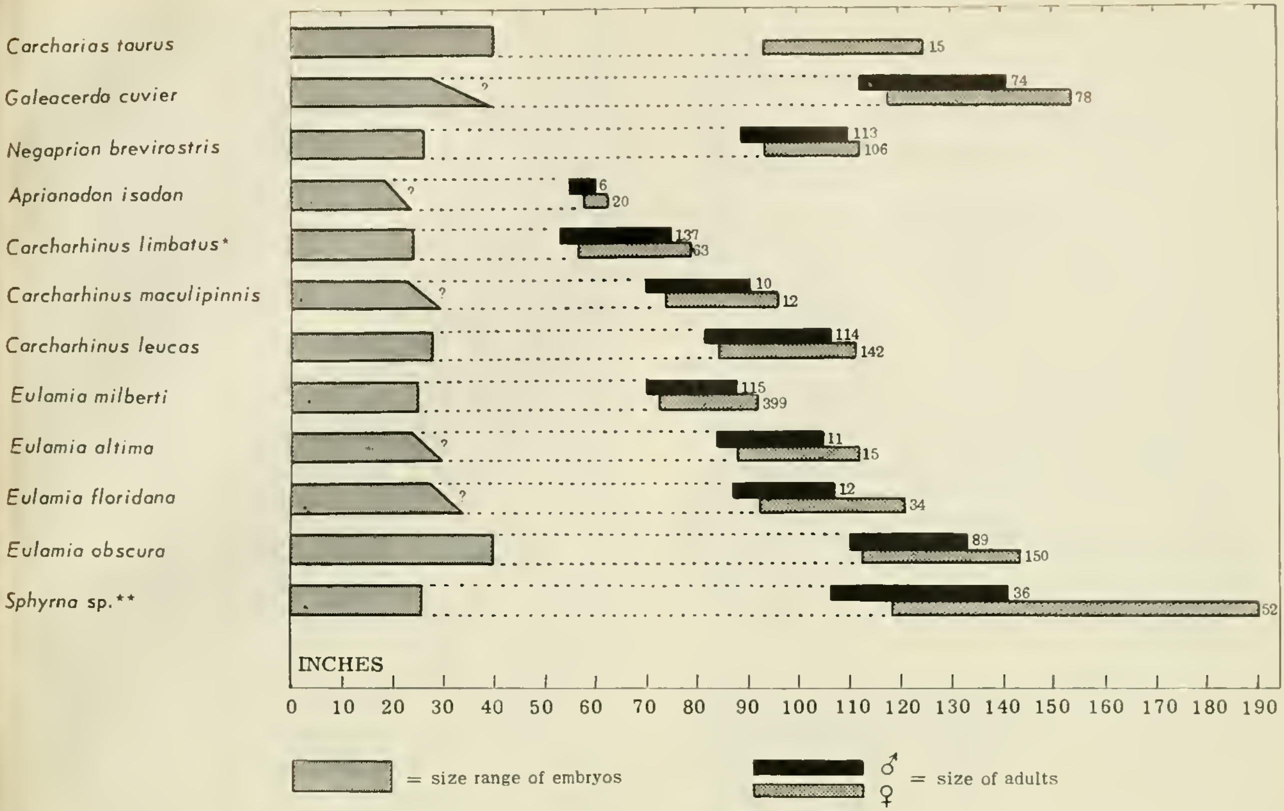

FIGURE 3.—Comparative sizes of adults and young of common large sharks found within the geographical range of *E. milberti.* The figures at the right indicate the number of specimens in the sample used to determine size range. The size ranges for embryos are estimates based on maximum observed lengths of embryos and minimun lengths of free-swimming young observed in Florida collections. (* Size range in Florida-Antillean specimens. Western Gulf of Mexico and Central American coast specimens are smaller and produce smaller young. The western stock may prove to be distinct and if so should take the name *Carcharhinus natator* Meek and Hildebrand. ** The great hammerhead of the West Indian region, following Bigelow and Schroeder (1948). The nomenclature is now unsettled. The name *Sphyrna tudes* is not available for the great hammerhead and probably should be replaced by *Sphyrna mokarran* (Rüppell).)

dental recruitment from the principal population. Within the expected vertical and geographical range of the species are some areas which appear to be avoided. It is well to mention again that the sandbar shark, like other large sharks, is not prevented by well-defined barriers from wandering out of its normal range.

The limits of distribution are therefore not sharply defined. Following the traditional pattern in descriptions of distribution it may be said that the sandbar shark, as represented by the western North Atlantic population, is common in summer off the Atlantic coast from Cape Cod to West Palm Beach, Fla., and in winter from the coast of the Carolinas around the tip of Florida to the gulf coast of Florida as far north as Tarpon Springs. It occurs uncommonly in the western part of the Gulf of Mexico and along the continental shores southward to Costa Rica. It is a casual visitor on the northern coast of Cuba and the western edges of the Bahama Banks. Its vertical range is from the shoreline out to 135 fathoms. It enters bay mouths but is not found in fresh waters.

The principal source of information on the distribution of the sandbar shark comes from the commercial shark fishery. Atlantic coast shark fishermen used bottom setlines more often than any other gear. Each unit of gear consisted of a main line of chain or wire rope a half-mile or more in length. This was set on the bottom, anchored at both ends with the anchors rigged with buoys so that the lines could be retrieved. Short, branch lines made of chain, each with a baited hook, were spaced at intervals of 20 to 40 feet along the central part of the main line. The typical unit had 100 hooks. Floating lines and anchored gill nets were also used occasionally in the fishery.

Positive information from the shark fishery on the distribution of *E. milberti* is quite voluminous and detailed. Systems of payments to fishermen required detailed records involving identification and measurement of all sharks landed by vessels of the principal fishing company. Altogether, records of landings of more than 100,000 *milberti* during a period of 15 years have been examined.

Information on the absence of *E. milberti* from specific areas has been difficult to assemble, but here also the records of the shark fishery supply most of the data. The species was first reported in the Florida area from correctly identified specimens after the commercial shark fishery began (Springer, 1938), so the earlier scientific literature has been useless in the establishment of the range of the species in the Florida area southward. Offshore records, from areas where water depths are more than 500 fathoms, are exclusively from catches made on tuna longlines used by the exploratory fishing vessel *Oregon* (for descriptions of this gear see Bullis, 1955, and Captiva, 1955). Some information on the distribution of the young was obtained from otter-trawl catches made by the exploratory fishing vessel *Delaware* off the coast of North Carolina. Additional scattered records were picked up from accidental catches made by commercial and sport fishermen who used various types of gear, from catches made by collectors fishing for aquarium specimens, and from biologists who captured specimens incidental to other collecting activities.

The area of greatest uncertainty is in the offshore and midwater range. Recent marine exploration has shown that substantial populations of large sharks, fishes, and invertebrates live in subsurface waters beyond the Continental Shelf where they have escaped the attention of naturalists. On June 11, 1954, the first *E. milberti* known from waters beyond the Continental Shelf was taken on a tuna longline hook at USFWS *Oregon* station 1099, 85 miles off the coast of Texas where the depth was approximately 600 fathoms. Since the hook was set to fish at about 30 fathoms, this shark, an adult male, was cruising in midwater. Throughout the second half of 1954, all of 1955, and the first part of 1956, longline fishing was carried on in the offshore waters of the Gulf of Mexico by the M/V *Oregon* and a few commercial vessels. Large numbers of sharks were taken, chiefly species known to be partly or entirely pelagic. No additional *milberti* were taken until early February 1955, when a commercial vessel caught two adult females about 50 miles off the northern edge of the Campeche Bank where depths were estimated to be more than 1,000 fathoms. These sharks were caught on longlines with hooks fishing not more than 50 fathoms deep. These three captures, outside the principal range, appear to have little significance in the general picture of the distribution of *Eulamia milberti*.

Factors affecting distribution

It may be assumed that water temperature and salinity are important in limiting the distribution of the sandbar shark and that there are other factors clearly influencing the movements and distribution of the species. The reaction of sandbar sharks to ocean currents, the availability of food, the relation between the growth rate or the reproductive pattern and the migratory movements, all appear to be important in forcing the species into a particular range. No data are available, however, to show the relative strengths of these conditions as determinants of the range of the sandbar shark.

The facts, from superficial examination at least, do not support the thesis that competition with other species is a powerful influence in the selection of a particular range. Young *Eulamia milberti*, for example, apparently cannot long survive where large *Carcharhinus leucas* in proportion to *milberti* are relatively abundant. The presence of large numbers of large *C. leucas* in the vicinity of the mouth of the Mississippi River seemingly does not deter gravid female *milberti* from moving into the area to give birth to young.

Whatever the particular reason or reasons may be, the general absence of young *milberti* in the Gulf of Mexico shows that conditions are unfavorable for them. Circumstantial evidence suggests that interspecies competition is responsible, because large *C. leucas* eat young *milberti.*

No explanation is apparent for the common occurrence of *E. milberti* along the continental shores and its absence from most of the West Indian shallow waters except that the species seems to have preferences for certain types of bottom. *E. milberti* is ordinarily not common in areas of coral reefs or where the bottom is rough. Since it is chiefly a bottom-dwelling species, it is not surprising that it would exhibit preference for one type of bottom over another. In its migratory passages around the southern tip of Florida and the Florida Keys, however, there appears to be active avoidance of the fringing reef. Here the migrating adults leave the relatively shallow areas they inhabit on both the east and west coasts of Florida and temporarily enter and feed in much deeper water.

Nursery grounds and distribution of young

The principal nursery grounds of the western North Atlantic population of *Eulamia milberti* lie in relatively shallow water along the Atlantic coast of the United States from Long Island to Cape Canaveral, Fla. This range may be extended slightly at its northern end to the south side of Cape Cod in favorable years but the southern limit is more definitely fixed. Not one young *milberti* has been taken south of Cape Canaveral, around the tip of Florida, or in the eastern Gulf of Mexico. On the east coast of Florida, south of Cape Canaveral, a few sexually immature *milberti* of almost adult size have been taken; but in this area adult *milberti* are common. A great quantity and variety of fishing effort has been concentrated south of Cape Canaveral on the Florida coast. The total absence of young *milberti* here is remarkable in view of the somewhat indefinite range limits of the adults.

A secondary nursery range apparently lies in the northwestern part of the Gulf of Mexico. It is indicated only by the capture of a few females with near full-term embryos near the mouth of the Mississippi River, the capture of a large *milberti* with nearly full-term embryos off the Texas coast (Henry Hildebrand, 1954), and a specimen 747 mm. (nearly 30 inches) from the Texas coast (Bigelow and Schroeder, 1948).

It is probable that gravid females wandering away from the principal range of the species give birth to young along the Mexican and Central American coast, but no records of the capture of young in this area have been found. Shark fishing on a small scale has been carried out over most of this area and catches have been examined at various points from the mouth of the Rio Grande River to Costa Rica; but excepting the Gulf of Campeche, no young *milberti* appeared.

The female *Eulamia milberti*, which move into the principal nursery areas to give birth to their young, do not remain there long and do not feed actively while there. This may explain the scarcity of records of captures of adult *E. milberti* along the Atlantic coast. Great South Bay, Long Island, is one of the nursery areas of *E. milberti*, and accounts of the appearance of females in the bay and birth of the young are given by Thorne (1916). Additional mention of the appearance of *E. milberti* in the Great South Bay area is made by Nichols (1918), who notes that the interesting fact about them is that the adults of the two sexes of the same species are almost never taken together near Long Island. Here the adult females are *E. milberti* and the adult males are *Carcharhinus leucas.*

Records of young sharks from Chesapeake Bay show that *E. milberti* gives birth to young in the bay in summer. William Massmann, of the Virginia Fisheries Laboratory, has kindly given me (in correspondence) records of *E. milberti* from the lower Chesapeake Bay. He says—

> Although young of this species are probably the most abundant shark in the Bay in summer, I would not say that it is numerous. * * * It is commonly caught by anglers and probably rather generally distributed in the lower Bay. I have not seen an adult in the Bay or any individual more than three and a half feet long.

After a comparatively brief period in shallow water or in the mouths of bays, perhaps at the beginning of cool weather, young *milberti* appear to move offshore. The only area from which young *milberti* are known in the winter season lies off the coasts of the Carolinas at depths out to 75 fathoms.

Distribution off Atlantic coast of the United States and in eastern Gulf of Mexico

The northern limit of the range of the sandbar shark is easily established. There are no reliable records of its capture from the Gulf of Maine (Bigelow and Schroeder, 1953), but south of Cape Cod it has been taken frequently but irregularly at Woods Hole, Mass. Numerous records of the species along the Atlantic coast of the United States are summarized by Bigelow and Schroeder (1948). Sandbar sharks may be said to be common in summer along the Atlantic coast of the United States from Long Island to the tip of Florida and in winter along the waters of the Continental Shelf off the Carolinas southward to the southern tip of Florida, in water of moderate depths in the Florida Straits and along the west coast of Florida northward to Tarpon Springs or the Middle Grounds (the rough bottom area south of Cape San Blas, Fla.). This area is the principal known range, but the species has also been taken in small numbers from the northern and western Gulf of Mexico, the western borders of the Bahama Bank, the northern coast of Cuba, and the Caribbean coast of Nicaragua and northern Costa Rica (fig. 4).

The hypothesis is advanced here that the sandbar sharks of the eastern and southern sides of the Gulf Stream in the Straits of Florida are casual visitors to those areas and that the stock of the northern and western parts of the Gulf of Mexico is a breeding stock which is not self-sustaining, but is recruited in part from migratory adults moving to the northern and western parts of the Gulf by mistake or through error in orientation and navigation during the regular winter migration of the principal stock.

The sandbar shark has been taken from the shallows along beaches out to a depth of about 135 fathoms. The young have been taken most often in shallow waters to depths of about 5 to 25 fathoms in summer, but in winter they move offshore to warmer water and depths as great as 75 fathoms off the Carolina coast.

The sandbar shark is known only from the shallower part of the Continental Shelf in the warmer months in the extreme northern part of its range. Probably the adults are more common off beaches than in major bays or inlets. Hildebrand and Schroeder (1928) found the species rather rare in Chesapeake Bay although more common than any other shark except the spiny dogfish. Radcliffe (1916) states that the species appears to be rare in the Beaufort, North Carolina, region. However, it was regarded as common in bays on the ocean side of Long Island from mid-June to mid-September, by Nichols and Breder (1927).

The apparent scarcity of adult *E. milberti* noted by Hildebrand and Schroeder and by Radcliffe is easily explained. It is possible that *E. milberti* enters the mouths of bays to give birth to young more frequently than records suggest. Female *Carcharhinus leucas* and *Negaprion brevirostris* move inshore and stop feeding for a short period at the time of the birth of their young, and immediately after the young are born the females move into comparatively deeper water. This may be a common habit among carcharhinids and certainly a very useful one to provide for survival of the species. The Long Island records are to a large extent based on harpooned specimens, and adult females should probably not be expected to be easily available to capture on baited hooks in areas where the young are born.

The best fishing depth for adult *E. milberti* from the Carolinas south to Miami was found by the commercial shark fishermen to be 15 to 30 fathoms. On this stretch of coast it was rarely if ever taken beyond 50 fathoms on bottom setlines and made up less than 5 percent of the catch on floatlines set beyond the 100-fathom curve.

Southward from Miami, *milberti* was rare among the keys, in Hawk Channel, or along the shallower portions of the reefs south of the Florida Keys. In the winter, a few appeared in catches made in the Northwest Ship Channel but, in general, these waters were left to other species. The sandbar sharks, however, were the commonest sharks on the bottom beyond the fringing reef out to depths of 50 fathoms and made up substantial portions of catches out to 100 fathoms. They were appreciably more numerous in catches off the lower keys where currents were not so strong. Northward from the keys along the west Florida coast as far as Tampa, *E. milberti* was found to be most abundant in depths of less than 30 fathoms.

Shark-fishing vessels operated out of Salerno, Fla., almost every day that weather permitted

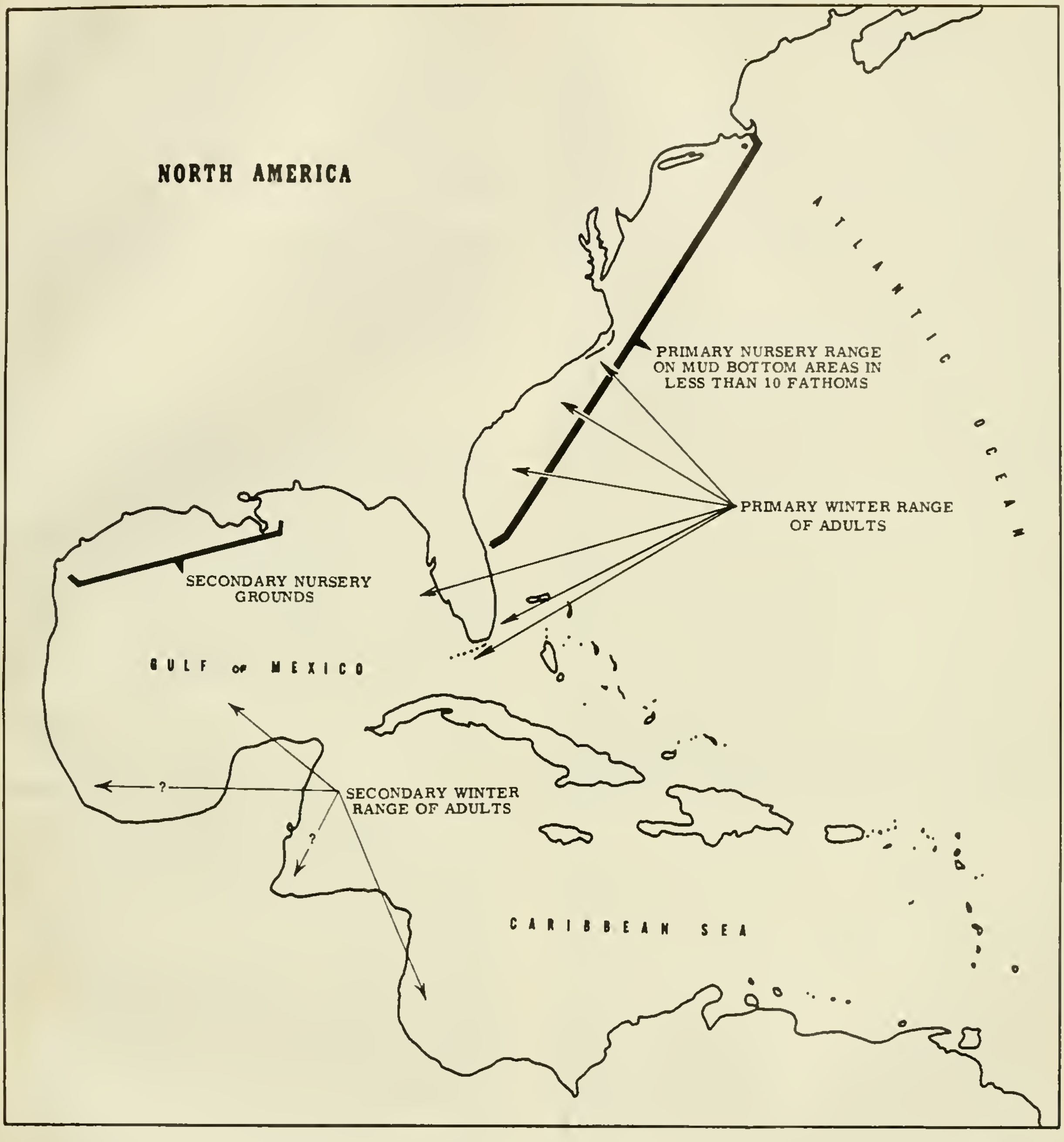
NORTH AMERICA
ATLANTIC OCEAN
PRIMARY NURSERY RANGE ON MUD BOTTOM AREAS IN LESS THAN 10 FATHOMS
PRIMARY WINTER RANGE OF ADULTS
SECONDARY NURSERY GROUNDS
GULF OF MEXICO
SECONDARY WINTER RANGE OF ADULTS
?
?
CARIBBEAN SEA

FIGURE 4.—Geographical distribution of the western North Atlantic population of the sandbar shark, *Eulamia milberti.*

from 1936 to 1950, except for parts of 1939 and 1940 when activities were suspended due to overproduction. These vessels landed their catches daily at Salerno where the sharks were identified, measured, and recorded. Catches included in the Salerno landings were made from Bethel Shoal, north of Fort Pierce, Fla., to the offings of Jupiter Light. Some details of these landings, showing catch per unit of effort, were reported in an earlier publication (Springer, 1951). These data show that at Salerno the highest average rate of catch of *E. milberti* occurred annually in the month of February and the lowest average rate of catch in September. These data concern only adult *milberti* and the comparatively few sexually immature *milberti* of adult size occurring with the adults.

On the west coast of Florida, shark-fishing vessels caught no *E. milberti* at all from May through November and reported their largest catches from January through March in each of several years for which data are available.

At Key West, Fla., high catch rates were obtained for *milberti* from deepwater sets made in the winter and early spring but catches at other seasons were poor.

High catch rates of adult *E. milberti* were obtained by shark-fishing vessels off the Carolinas in September, and from 1946 to 1949 one or two of the more able shark-fishing vessels followed the fishing for adult *milberti* southward, arriving off Salerno in January or February.

Scouting by shark-fishing vessels showed that some adult *milberti* were present in each month of the year along the Atlantic coast between the latitudes of Charleston, South Carolina, and Miami, Florida. Although *E. milberti* was the principal species sought in this area, other species contributed variously to the value of the total catch. Table 2 shows the comparative availability of large sharks to the kinds of fishing gear employed in the Salerno area in the late spring.

Distribution in Bahamas and West Indies

E. milberti is common only on the western side of the Gulf Stream. On the eastern side of the stream, it is replaced by *E. falciformis* as the common inshore *Eulamia*. The wandering of *milberti* into the Antillean area may be quite limited. There are no records of *milberti* eastward through the West Indies nor from the southern shores of Cuba. A shark fishing operation on the eastern part of the Bahama Bank in the period from 1947 to 1949 did not take *milberti*.

E. falciformis was reported by Evermann and Marsh (1902) from Puerto Rico; by Beebe and Tee Van (1928) from Port-au-Prince Bay, Haiti; by Nichols (1929) from Puerto Rico; and by Backus (1957) from open sea situations east of the Gulf Stream. None of these authors noted the presence of *E. milberti*.

Frank Mather III has told me in correspondence of the capture of *E. falciformis* and *E. floridana* from the vicinity of St. Croix and St. Thomas in the Virgin Islands. Mather's fishing operations covered the depth range in which *E. milberti* would be expected if its geographical range extends through the West Indies and if the absence of *milberti* follows the usual pattern in the West Indies.

Table 2.—*Sharks taken by commercial fishing vessels in the Salerno-Fort Pierce area (Bethel Shoal to Jupiter Light) and landed at Salerno, Fla., in May and June 1945–46*

[1 to 3 vessels; only sharks with hide length of 55 in. or more included; fishing depths from 18 to 40 fathoms]

Species	Number of sharks	
	1945	1946
Eulamia milberti (Müller and Henle), sandbar shark	1,515	987
Sphyrna sp.,[1] hammerheads	323	268
Eulamia obscura (LeSueur), dusky shark	269	94
Eulamia floridana (Bigelow, Schroeder, and Springer), silky shark	220	191
Galeocerdo cuvier (LeSueur), tiger shark	68	64
Carcharhinus leucas (Müller and Henle), bull shark	61	41
Negaprion brevirostris (Poey), lemon shark	20	19
Carcharhinus sp.,[2] blacktips	3	16
Ginglymostoma cirratum (Gmelin), nurse shark	2	6
Carcharodon carcharias (Linnaeus), great white shark	2	5
Isurus oxyrinchus Rafinesque, mako	0	2
Unidentified	120	2

[1] 3 species; station records do not distinguish kind.
[2] 2 species; station records do not distinguish kind.

That the Gulf Stream is not itself a barrier to *E. milberti* is apparent from the occasional captures along the Bahama Banks and off the northern coast of Cuba. It is possible that large numbers of migratory sharks may wander away from normal migratory routes at times when unusual conditions prevail. Certainly a few *milberti* cross the stream.

From May 18, 1948, to July 8, 1948, I undertook a program of experimental shark fishing along the western edge of the Bahama Bank from Riding Rock northward. Fishing operations were carried out from a base at the Lerner Marine Laboratory of the American Museum of Natural History at Bimini, using a fishing vessel and gear provided by the Shark Industries Division of the Borden Co. Fishing was carried on chiefly by bottom setlines at depths from 10 to 200 fathoms, but some floating lines were used to assure collection of as wide a variety of sharks as possible. Sets included some made at various levels along the extremely precipitous slope of the bank, which drops off abruptly from about 20 fathoms down to the floor of the Gulf Stream channel where depths are more than 150 fathoms.

During the entire fishing period along the Bahama Banks only 14 *E. milberti* were caught in the lot of 447 sharks. Of the total, 197 were reef sharks, *Eulamia springeri* (Bigelow and Schroeder).

TABLE 3.—*Sharks taken in exploratory fishing from the* Dusky *along edges of northwestern Bahama Banks, May 18 to July 8, 1948*

Species	Number of sharks taken in—	
	Bimini area (20–200 fathoms)	Walker Key (10–100 fathoms)
Eulamia springeri (Bigelow and Schroeder), reef shark	10	187
Galeocerdo cuvier (LeSueur), tiger shark	60	13
Eulamia obscura (LeSueur), dusky shark	46	5
Negaprion brevirostris (Poey), lemon shark	2	18
Eulamia altima Springer, bignose shark	17	2
Eulamia floridana (Bigelow, Schroeder, and Springer), silky shark	15	0
Eulamia milberti (Müller and Henle), sandbar shark	10	4
Hypoprion signatus Poey, night shark	12	2
Scoliodon terra-novae (Richardson), sharpnose shark	11	3
Ginglymostoma cirratum (Gmelin), nurse shark	2	3
Sphyrna lewini Griffith, southern hammerhead	5	2
Hexanchus sp. (not *H. griseus*), little cowshark	3	0
Carcharhinus limbatus (Müller and Henle),[1] little blacktip	3	1
Sphyrna sp.,[2] great hammerhead	1	2
Carcharhinus leucas (Müller and Henle), bull shark	0	3
Mustelus canis (Mitchill), common smooth dogshark	1	0
Pterolamiops longimanus (Poey), whitetip	1	0
Carcharhinus maculipinnis (Poey), big blacktip	0	1
Carcharhinus acronotus (Poey), blacknose shark	1	0
Eulamia sp., undetermined	1	0

[1] Antillean form.

[2] Nomenclatorial status of this species not determined.

During the same season of the year in which the exploratory fishing was done, a great number of sharks were landed across the Gulf Stream at Salerno, Fla., about 80 miles from the northern end of our Bahama fishing area. But more than half of them were *E. milberti*, and no *E. falciformis* was landed. Results of the Bahama fishing are summarized in table 3, which shows catches made in two areas off the Bahama Banks. For purposes of camparison, catches made in the Salerno–Fort Pierce area in May and June 1945 and 1946 are shown in table 2. The two fishing operations are not exactly comparable, of course, not only because they were carried on in different years but because the Bahama fishing was essentially exploratory while the Salerno–Fort Pierce fishing was a part of a continuing commercial operation concentrated in limited depths and locations. Exploratory fishing with sets scattered in different depths and locations off Salerno would presumably produce a few *E. springeri* because there are normally a few to be found along inshore reefs adjacent to the St. Lucie Inlet at Salerno. This is a poor fishing spot, however, so the commercial vessels rarely caught *springeri*.

Distribution in western Gulf of Mexico and western Caribbean

Positive knowledge of the distribution of *Eulamia milberti* in the western part of the Gulf of Mexico and along the Caribbean coast of Central America is based on records of 8 gravid females off the Mississippi River delta, 1 gravid female and 1 young male from the coast of Texas, 1 adult male and 2 adult females from the south-central part of the Gulf of Mexico over deep water, and 51 adults from the Caribbean coast of Nicaragua and Costa Rica.

From the mouth of the Mississippi River eastward and southward around the Gulf to the vicinity of Tarpon Springs on the Florida west coast, *milberti* appears to be absent or at least rare from inshore waters out to 30 fathoms. No catches were reported by shark fishermen and no specimens were seen. I should note that while employed in the shark fishery, seasonal shark-fishing stations were maintained at various times at all of the fishing ports of any consequence from the mouth of the Mississippi River around the tip of Florida to the Carolinas. I visited all of these stations frequently and sometimes participated in fishing operations. The presence of *milberti* in appreciable quantity would almost certainly have been noted in catches from the stations at Panama City and Carrabelle, Fla., had specimens been taken.

It is not possible to present a meaningful account of the sandbar shark, *Eulamia milberti*, without frequent reference to the bull shark, *Carcharhinus leucas*, and its fresh-water representative, *Carcharhinus nicaraguensis* (Gill and Bransford). The sandbar shark has been confused with the bull shark because of the peculiar manner in which their ranges overlap. In addition, bull sharks appear to be the most important of the predators on young sandbar sharks and the primary factor that prevents *E. milberti* from extending its nursery range into otherwise suitable areas in tropical seas.

As has already been noted, bull sharks are found along the Atlantic coast as far north as Long Island but increase in numbers somewhat in the latitude of Salerno, Fla., where, as noted in table 2, they were sixth in number of large sharks landed by the shark fishery. The abundance of bull sharks at various locations in the Gulf of Mexico varies seasonally, but from the vicinity of Apalachicola, Fla., westward along the northern coast of the Gulf of Mexico and southward along the coasts of Central and South America as far at least as French Guiana, bull sharks form the major part of catches of large sharks made by shallow-water setlines in some seasons. Table 4 shows the comparative frequence of capture of large sharks during a test-fishing period off the mouth of the Mississippi River.

TABLE 4.—*Large sharks taken from the* Joe Leckich *on bottom lines set in 5 to 35 fathoms off the mouth of the Mississippi River, June 25 to July 29, 1947*

Species [1]	Number of sharks	Average weight of liver (lb.)
Carcharhinus leucas (Müller and Henle), bull shark	275	38
Eulamia obscura (LeSueur), dusky shark	83	53
Galeocerdo curier (LeSueur), tiger shark	56	129
Carcharhinus limbatus (Müller and Henle), little blacktip [2]	47	3
Sphyrna sp., great hammerhead	9	49
Carcharhinus maculipinnis, big blacktip	8	13
Eulamia milberti (Müller and Henle), sandbar shark	8	14
Carcharias taurus Rafinesque, sand shark	7	26
Negaprion brevirostris (Poey), lemon shark	4	20
Sphyrna lewini Griffith, southern hammerhead	3	12
Eulamia floridana (Bigelow, Schroeder, and Springer), silky shark	1	16
Eulamia springeri (Bigelow and Schroeder)	1	4

[1] Also taken but not recorded because of small size: several *Scoliodon terra-novae* (Richardson), *Carcharhinus porosus* Ranzani, and *Mustelus canis* (Mitchill), and one young *Ginglymostoma cirratum* (Gmelin).

[2] Continental form—typical of western Gulf of Mexico.

The eight *E. milberti* were adult females and five of them were gravid. Since *milberti* has liver oil of comparatively higher potency than the oil from other species in the area, a special effort was made to catch them in subsequent, larger scale fishing efforts. Nevertheless, catches of *milberti* were not made later during 1947 and commercial fishermen operating in the area reported sandbar sharks absent in 1948 and 1949. The few records of *E. milberti* from offshore Gulf waters would not be important except that they serve to show the species can move into and across deep areas of the ocean. Off the Atlantic States there has been comparatively little longline fishing beyond the Continental Shelf and there are no records of *milberti* from deep water. There are, however, records of catches of *Eulamia falciformis* (Müller and Henle) and *E. obscura* from longline sets made by the exploratory fishing vessel *Delaware* beyond the limits of the Continental Shelf off the Middle Atlantic States. These two species are also reported by Backus (1957) from the Atlantic beyond Continental Shelf limits.

A lot of 51 adult sandbar sharks was taken by Captain B. W. Winkler from off the Caribbean coast of Nicaragua and Costa Rica. This group included all of the sandbar sharks in a collection of 854 sharks of all species which Captain Winkler measured and recorded for me from September through December, 1948. The most interesting feature of this collection of *E. milberti* was that it was made up of approximately equal numbers of adult males and females (26 males and 25 females).

The shark fauna of the area as represented by Captain Winkler's collections included a large number of species that are predatory on sharks of the size of young *E. milberti*. The following sharks were taken:

Species:	*Number*
Carcharhinus,[1] chottos or bull sharks	421
Galeocerdo cuvier (LeSueur), tiger shark	85
Eulamia obscura (LeSueur), dusky shark	76
Eulamia floridana (Bigelow, Schroeder, and Springer), silky shark	70
Carcharhinus limbatus (Müller and Henle),[2] little blacktip	54
Eulamia milberti (Müller and Henle), sandbar shark	51
Sphyrna sp. (not determined), hammerhead shark	27
Eulamia sp.,[3] reef sharks	25
Scoliodon sp., sharpnose shark	15
Hexanchus sp.,[4] cow sharks	13
Ginglymostoma cirratum (Gmelin), nurse shark	3
Eulamia altima Springer, bignose shark	2
Negaprion brevirostris (Poey), lemon shark	1
Undetermined [5]	4

[1] Either *C. leucas* (Müller and Henle) or *C. nicaraguensis* (Gill and Bransford) or both.

[2] Continental form.

[3] Probably *E. springeri* (Bigelow and Schroeder) or *E. falciformis* (Müller and Henle).

[4] Includes two species.

[5] Possibly a small species of *Galeorhinus*.

A few days' fishing with bottom longlines along the outer edge of the Continental Shelf off northern Nicaragua and on Serrana and Seranilla Banks in February 1949 failed to produce *E. milberti* or any adult sharks, but moderate numbers of young *E. floridana* were taken.

As a grader and buyer, I examined several lots of dried shark fins said to have been taken off the coasts of Colombia and Venezuela. *E. milberti* fins were not noticed although it is possible that a few might have been overlooked. The fins of *E. milberti* adults (pectorals, first dorsal, and lower caudal lobe) are more desirable for commercial purposes than the fins of some other species because they are thicker and have a relatively large proportion of the material used for shark-fin soup. Shark fishermen with whom I talked and who would recognize *milberti* also reported the absence of the species from their catches made off Colombia and Venezuela. Thus, evidence for the occurrence of *E. milberti* in the southwestern Caribbean, while not very satisfactory, is negative.

MIGRATION

It is probable that the migrations of *E. milberti* are of two kinds. One is simply the gradual withdrawal of the sharks from waters that become too cold or too warm—a movement that is accompanied by normal feeding activities and is characteristic of immature sharks. The other is a movement, generally, over a greater distance that may or may not be induced by temperature changes. The general patterns of the major movements of adult sandbar sharks suggest that ocean currents greatly influence the direction and extent of the movements.

It is necessary to consider the migratory movements of the adult male, the adult female, and the immature *Eulamia milberti* separately. We may look upon the Atlantic coast from the vicinity of Charleston, South Carolina, to the northern part of Florida as the core of distribution of the principal stock of the western North Atlantic population because it is only in this area that all three groups are known to be found. This may mean merely that in this area there is overlapping distribution. We know that the adult females go as far north as Long Island to give birth to young in summer and in some years even farther, to the vicinity of Cape Cod. There are no data to show whether the adult males or nongravid females move northward into the portion of the species' range lying north of the Carolinas. All that is known of the distribution of the young is that the young are born in water of moderate salinity from Cape Canaveral to Cape Cod and that some of them move in winter into the comparatively warmer offshore water found at depths of 50 to 75 fathoms on the Carolina coast. Until the young sharks reach adult size they do not take part in the long southern migration characteristic of adults or move south of Cape Canaveral. One capture of a lot of nearly 200 young off North Carolina indicates that the young occur in schools of both sexes and of mixed sizes.

Migratory movements of adult *E. milberti* south of Cape Canaveral are more clearly outlined from the data available from the shark fishery. The annual southward movement appears to be coincidental with the beginning of cooler weather and to be accelerated by cold snaps.

A very much larger number of adult female sandbar sharks were taken than adult males by the Florida shark fishermen. This and the tendency to segregation by sex, will be discussed later in connection with reproduction. But it should be pointed out here that no adult males are recorded from inshore nursery grounds and probably occur there but rarely. In the Florida shark fishery, adult males of most species brought more money than adult females and were particularly sought by fishermen. The fishermen were convinced by observation that adult males of most species including *milberti* were usually in deeper and cooler water than the females, that they usually preceded the females in migration, and that they usually were to be found in more compact aggregations so that fishing was best where males could be found. Such figures as are available bear this out. A rationale for this condition is suggested by the thermal sensitivity (decreased fertility with application of heat) of the male germ plasm among vertebrates in general (see Cowles, 1945).

The sandbar shark is properly considered a "ground shark" and is rarely to be seen from the surface except when it comes into shallow water. An exception to this occurs off Salerno immediately following periods of especially cold winter weather north of that area. At such times, when weather and water surface conditions permitted observations from a boat, large schools of *milberti* were to be seen headed south, swimming at about 3 to 5 knots 5 to 10 feet below the surface, but where water depths were about 20 fathoms or more. Shark fishermen have told me, and my own experience bears this out, that it is useless to try to follow these sharks or to try to divert them by chumming or by setting lines ahead of them. The appearance of southbound schools at Salerno was generally accepted as a harbinger of better fishing a few days later.

The southbound migratory movements of *E. milberti* at Salerno were inshore and within the southbound eddy of the Gulf Stream; northbound movements were not observed. It is suggested that these movements were either offshore movements or slower movements of more diffuse aggregations. Northbound movements offshore would be aided by the Gulf Stream. An hypothesis which may be more convenient than significant is that *E. milberti* tends to follow currents in migration and if the currents are strong does not go against them. Of course, sharks would not make appreciable headway against the current at the surface near the axis of the Gulf Stream without vigorous and persistent effort. The sandbar shark does appear to take advantage of eddies or countercurrents and the fishing plans of some of the more successful shark fishermen were based on an assumption that the shark's seasonal movements would follow the currents available at the time.

The distance traveled by various segments of the population probably does not extend from one end of the geographical range of the species to the other. From the southern end of the nursery range of the principal stock at Cape Canaveral, a seasonal gradient of availability was shown by catch per unit-of-effort data. This availability decreased in summer southward and around the tip of Florida to the west coast of Florida where the species was completely absent from summer catches. Thus, the minimum migratory travel of the part of the stock reaching the vicinity of Tampa would be approximately 600 miles. Catches of *E. milberti* throughout the area beyond the southern end of the nursery range reach their highest peak in midwinter. Catch per unit-of-effort data previously published (Springer, 1951) show the catch of *E. milberti* at Salerno, Florida, as decreasing from 4.8 fish per 100 hooks for February to a low of 1.1 per 100 hooks for September. A cold upwelling over the narrow Continental Shelf immediately north of Jupiter Light usually occurs in June or July. It is probably of brief duration but annually stuns great quantities of fish, although the sharks are not affected. This phenomenon coincides with spectacularly good shark fishing and possibly also with considerable mating activity on the part of *E. milberti*. This may give some bias to Salerno catch per unit-of-effort figures for early summer.

REPRODUCTION

Courtship and mating

I have seen neither the courtship nor mating of *Eulamia milberti*. The general pattern may be constructed, however, from fragments of information and from inferences based on the few facts known about related large sharks. The comparative morphology of the secondary sexual apparatus of male sharks has been given comprehensive discussion by Leigh-Sharpe in 11 papers. The functions ascribed by Leigh-Sharpe in three of these papers (1920, 1921, and 1924) to the various parts of the apparatus in carcharhinid sharks are in general accord with my observations on *Galeocerdo*, the tiger shark. The courtship patterns in *Galeocerdo*, *Eulamia milberti*, and other large carcharhinids probably do not differ greatly.

A brief outline of the mechanics of fertilization in the carcharhinid sharks is included here to orient the reader in following some of the inferences made in later discussion of differential death rates in the sexes. Carcharhinid sharks are born alive and fertilization is internal. Paired intromittent organs of the male known as claspers are supported by cartilages. Immediately following the rapid enlargement of the testes, which occurs at maturity, layers of calcification appear at the surface on the principal clasper cartilages. At this time the claspers become semirigid except at the basal area of attachment of the claspers to the base of the pelvic fin adjacent to the cloaca. The tip of each clasper, however, is expandible. When expanded, the cartilages of the tip are transverse to the main axis of the clasper and open as the ribs of a fan. The expanded tips are thought to serve both to hold the oviducts of the female open and to prevent withdrawal of the claspers because of the rigid cartilages in a transverse position. The very large clasper siphons are a distinguishing and peculiar feature of the apparatus in male carcharhinids. These siphons are a pair of separate sacs lying just under the skin of the belly on either side of the midline and extending from the pelvic to the pectoral areas. They function as reservoirs for the sea water used to flush the male sex cells from the bases of the claspers into the oviducts of the female during mating. The siphons may hold a large amount of sea water, as much as 2 gallons in *Galeocerdo.* The siphons do not ordinarily contain the sea water which is presumed to enter the siphons during the period immediately preceding mating.

During the mating season the area at the bases of the claspers of the larger carcharhinids exhibit extraordinary vascular congestion. Characteristically, in male *Galeocerdo*, a mass of very soft spongy tissue appears around the cloaca. This is present to a lesser degree in the smaller carcharhinids such as *E. milberti.* Unusual congestion, edema, and subdermal hemorrhage at the base of the claspers are evidences of courtship activity on the part of the male.

Large sharks are not highly maneuverable and cannot swim backward, so it is necessary for the claspers to rotate and point forward during mating. Since the muscle system in the typical carcharhinid clasper seemed functionally inadequate or feeble, I carried out an experiment which incidentally revealed the probable method by which the clasper siphons are filled with sea water. I obtained an adult male *Carcharhinus limbatus* about 5 feet long and evidently in mating condition. The choice of species was dictated by circumstances, one of which was the fact that a 5-foot shark was as large as I could manage. By injecting a considerable quantity of an isotonic solution into the caudal vein, I was able to induce the claspers to assume the normal mating position. This action caused the claspers to revolve inward and forward. As the claspers moved into a forward pointing position, a funnel, formed by a membrane supported by rods of cartilage, opened at the base of each clasper. The mouth of the funnel was also directed forward and the constricted end led into the siphon. The caudal vein was plugged experimentally to hold the claspers and funnel in position and the shark was moved forward as rapidly as possible through the water. This caused the clasper siphons to fill with water. Application of additional pressure to the caudal vein resulted in complete expansion of the fanlike tip of each clasper.

The course of courtship and mating in all of the larger carcharhinids including *E. milberti* probably follows the pattern in which the male persistently follows and occasionally bites the female on the back until she swims upside down. Both claspers probably function at the same time, one entering each oviduct of the female by way of the lateral opening from the cloaca. The contact of the two sharks may be presumed to force the sperm-ladened sea water from the siphons into the oviducts.

The mating pattern has been given in some detail to emphasize the point that mating is very complicated in carcharhinids, and that the mechanical difficulties are compounded among the larger species by their greater weight and lesser maneuverability.

Time of mating

The approximate period of the mating season is established by the appearance of males with enlarged testes and also with some evidence of vascular congestion of the pelvic-fin area and by the appearance of females with eggs of full size in the ovaries (about 1 to 1¼ inches in diameter in *E. milberti*). In the vicinity of Salerno, Fla., mating of *E. milberti* evidently takes place in the spring or early summer. Males appear commonly in inshore catches after the first of February but remain segregated for some time. Catches of both sexes indicating mixed schools are more frequently made in April and May than in other months. After May, male *E. milberti* are relatively scarce in Salerno catches. Among carcharhinids, the males may stop eating during the courtship period. This is an inference drawn partly from the general reduction of catches of males on baited hooks during mating seasons, partly from the observed smaller size of the livers of males immediately following the mating season, and partly from observations on the mating activity of *Galeocerdo.*

Fertilized eggs and the smallest detectable embryos were observed first in Salerno catches from the first part of July to the first part of August. The time of mating can be established with more precision, however, by observation of the time of appearance of the fresh courtship scars on the females. Scars, tooth marks, and small open wounds produced by shark teeth are commonly found on adult female carcharhinids and are generally restricted to the dorsal surfaces between the two dorsal fins. These are never present on males or immature females and are obviously produced during courtship. Scars or wounds are not always present on gravid females or at least are not always detectable but were found on about half the gravid *E. milberti* taken at Salerno. The coexistence of old and completely healed scars with fresh scars on some females is one bit of evidence that female *E. milberti* produce more than one litter of pups in a lifetime.

All available evidence points to the month of June as the time of maximum mating activity of *E. milberti* in southeastern Florida waters. It has already been pointed out that males were rarely taken during the month of June when mating activity is assumed to be at a peak. There is some evidence from catches that the males were present in substantial numbers at that time. From 3 to 5 percent of the catches of the better fishermen at Salerno, who kept their hooks very sharp, were snagged sharks; that is, the sharks were caught by hooks in the fins or tails or occasionally in other parts of the body but not in the mouth. More males were caught in this way during June than were hooked by mouth.

Development of the embryo

In *E. milberti*, as in other carcharhinids, it is presumed that fertilization occurs after the large egg leaves the single functional ovary. It is also presumed that fertilization occurs before the egg has been moved through a shell gland. Shell glands are located near the anterior end of each of the two functional oviducts. In passing through the shell-gland area of an oviduct, a single egg is enveloped by a diaphanous tubelike shell capable of great expansion to accommodate the growth of the embryo to a very large size. The nutrient material from the egg yolk is sufficient only to provide for early growth of the embryo and to supplement nutrient materials necessary for intermediate growth. The means by which nourishment is supplied to the growing embryos probably varies in different species of carcharhinids, but in species of *Eulamia*, three principal methods appear to be involved. In addition to that supplied by the yolk some absorption of nutrient material from fluids in the oviducts may be assumed to take place. This would appear to be necessary to provide sufficient material to carry the embryo to a length of about 12 inches at which length the pseudoplacenta is formed from the yolk sac.

My observations ~~on the~~ embryology of the sandbar shark are limited to general notes on the external appearance of the eggs and embryos at several stages during development.

The spherical, unfertilized eggs in the single functional ovary reach a diameter of 1 to 1¼ inches. In winter and early spring, large numbers of adult females not carrying embryos were found to have developing eggs ½ to ¾ inch in diameter in the ovaries. In a few instances, females taken in July and August were found with eggs of maximum size in the ovaries as well as fertilized eggs in the oviducts. In the greatest disparity of development noted, there were two large yellow eggs remaining in the functional ovary while embryos in the oviducts ranged from less than 6 mm. to 10 mm. in length.

A female *milberti*, 6 feet 7 inches long collected off Salerno on July 2, 1948, in 25 fathoms, was typical of a series taken in early July of that year. This female contained 10 egg cases, 5 in each oviduct; no large eggs remained in the functional ovary. Each stringlike egg case was about 120 centimeters long, with thin membranous, amber-colored, transparent walls. A single yolk was contained in one expanded oval section of each egg case. The expanded section, approximately 6 cm. long, was located about 10 to 12 cm. from one end of the egg case. This section also contained a clear fluid in each of 8 of the egg cases that had developing embryos 9 to 13 mm. long. The remaining 2 egg cases, one anteriorly in each oviduct, contained milky fluid and there was no evidence of fertilization nor development of the single egg yolk contained in each. The section of the egg case occupied by the embryo, spherical yolk, and clear fluid was held in shape by two longitudinal folds and by folded constrictions of the egg-case membrane at either end. The egg case could, however, be unfolded and expanded with relatively light internal pressure.

The egg case surrounds the embryo until birth and unfolds or stretches to accommodate the developing embryo. When the embryo reaches full term the pseudoplacental mass extends outside of the eggshell membrane, but my notes do not indicate at what point the pseudoplacenta functions outside of the shell membrane. The amount of clear fluid within the shell increases as the embryo grows. It is present at the time the embryo reaches the approximate size at which the young are born—24 inches in the Florida area. External gills were noted on embryos up to about 4 inches but were absent on 4¼- to 5-inch embryos. Some yolk was found remaining in the pseudoplacental apparatus in embryos that had reached a size of 12 inches, but yolk material was entirely absent from the well-developed, yolk-sac placental apparatus of embryos 15 inches long. As the embryo grows, the yolk or attachment of the pseudoplacenta lengthens. In *E. milberti* and in other western North Atlantic *Eulamia* the yolk stalk has no structural embellishments at any stage in its development insofar as I have been able to discover. Structures of this kind occur in some species of hammerhead, *Sphyrna*, but differ in the various species. When embryonic *E. milberti* are near full term the stalk (pseudoplacental attachment) is easily broken at the point of attachment to the embryo. The scar of this attachment remains clearly visible until the young shark has attained an inch or more of postnatal growth.

Normally the large eggs in the ovary of *E. milberti* are bright yellow; but white eggs, suggesting some pathological condition, were found a few times in the fall. White eggs were noticed less frequently in *E. milberti*, however, than in *Eulamia obscura*, *Carcharhinus leucas*, or *Sphyrna* sp. In these last three species, white eggs were noticed in exceptionally large sharks (*E. obscura* and *Sphryna* sp.) and deformed sharks (*leucas*). No excessively large deformed or obviously diseased *milberti* were seen in examinations of many hundreds of adult females. Dead embryos were noted occasionally but not frequently in *E. milberti* and these were generally 10 to 15 inches long, that is, at about the size at which the egg yolk would be completely absorbed. The dead embryos sometimes appeared to be dehydrated but there was no noticeable putrefactive decomposition.

Number of young in litter

In an earlier publication (Springer, 1940), I reported the collection of 13 litters of *Eulamia milberti* pups from Englewood, Fla. In this lot 59 were males and 63 were females. Another series of 28 litters from the west coast of Florida had 130 males and 130 females. A third series of 24 litters from the east coast of Florida included 116 males and 112 females. The number of embryos in each litter varied from 1 to 14 but the modal number was 10 and the average number was 9.

The available data do not show an increase in the number of young with increased size of the mother as reported for some other genera (Backus et al., 1956). In *Eulamia milberti*, however, the size range of adult females is not great and such a correlation, if it exists, would be difficult to demonstrate.

Species of *Eulamia* taken in the Florida region other than *milberti* all frequently carry 10 embryos to full term. The average number of embryos to the litter for these other species is less than 9, which is the average litter number for *E. milberti*. All of the other Florida species of *Eulamia* are somewhat larger than *milberti* and the largest species, *Eulamia obscura*, has the smallest average number of embryos to the litter. In *E. obscura*, pups were often found only in one of the oviducts. This suggests the possibility that fertilization was effected only through one oviduct. Various other observations on the location and numbers of embryos in *E. obscura* and other Florida *Eulamia* lead to the conclusion that the normal maximum [usual] number of young in each species is 10 plus or minus 2, but that actual numbers are progressively smaller the larger the mother.

Length of young at birth

Consideration of all of the available data places the time of birth from March to early August and the size at birth from 17 to 25 inches. The length at birth of 24 inches seems, however, to be the best estimate for the young born in northern Florida waters. Smaller young and a somewhat later birth date may be characteristic of the part of the population in cooler waters. An estimate of the gestation period based on southern Florida specimens is 9 months with limits of the estimate 8 to 12 months. Some variation might reasonably be expected to result from differences in water temperature during development.

Table 5.—*Embryos of* Eulamia milberti, *by size group and month, from females collected off the southeast coast of Florida between Fort Pierce and Tortugas, 1946–49*

Average litter length	Number of litters											
	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June
1 inch and under	5	7										
2 inches		5										
3 inches		4										
4 inches		6										
5 inches		1		1								
6 inches		1										
7 inches												
8 inches			2	2								
9 inches				1								
10 inches				1								
11 inches				1								
12 inches			1		1							
13 inches								1				
14 inches					2					3		
15 inches					2			1		27		
16 inches					1		1	1		11		
17 inches						6	1					
18 inches						7	4	1				
19 inches						4	6	3	1			
20 inches						3	1					
21 inches										1		
22 inches										5		
23 inches									1	1	4	
24 inches									1		5	1

Table 5 shows the length distribution by months of embryos of *E. milberti* from off southeastern Florida. It is possible that some of the variation in length of embryos near full term is due to inclusion in the sample of measurements from females of widely differing geographical origin, for example northern Florida and Chesapeake Bay.

At Salerno, Fla., 5- to 10-mm. sandbar shark embryos were found commonly in July and August but no large embryos were seen during these months. In June only a few among the large numbers of adult female *E. milberti* landed at the Salerno dock contained embryos and the few that were found were 24 inches long. Since no free-swimming young were taken at Salerno or around southern Florida, estimation of the size at birth in this area depends entirely on determination of the maximum length of embryos. Records of young *E. milberti* from Cape Canaveral, about 60 miles north of Salerno, northward are common. Twenty-four-inch embryos from south Florida were found to be most common in May but substantial numbers were seen in April, and one set of 24-inch embryos was taken from a female collected off Marquesas Island in the Lower Florida Keys in March. Eight adult female sandbar sharks were taken on July 2, near the mouth of the Mississippi River. Of these, five contained 24-inch embryos and one had 25-inch embryos. Two had evidently given birth to young just before they were caught.

Hildebrand and Schroeder (1928) report six *E. milberti* in their collection from Chesapeake Bay 17¾ to 25½ inches long. Presumably these were not embryos. Records furnished by William H. Massmann (in correspondence) for young Chesapeake Bay *milberti* include specimens from 21¾ to 28 inches that were taken in 10 collections from June 7 to October 7. Massmann's series is not large enough to establish progressively larger size with later dates.

Some young *E. milberti* may be born prematurely at lengths of less than 20 inches either because of crowding, in large litters, or extraordinary activity on the part of the mother. Captures of very small young in otter trawls, for example, might result from the entry of the mother into the net followed by a successful struggle to escape. This could bring about premature birth of one or more young which might be left in the net.

Nichols and Breder (1927) note that females carrying young were taken in Great South Bay, Long Island, from June 22 to August 5. Also they state, when released the young were about 22 inches long and weighed 2½ pounds. One of about 3 feet seen in Sandy Hook Bay as early as June 9 may have been of the preceding year. In September 1924, five young ranged from 24⅞ to 26 inches in total length. Bigelow and Schroeder (1948) summarized the indications of size at birth from various Atlantic coast records north of Florida in approximately the same way. It is reasonable to expect that *E. milberti* at birth may be somewhat smaller in the northern part of its range than in the southern part and that the growth rate in cooler waters is slower.

Abnormal embryos

In the late spring of 1942 I collected at Salerno, Fla., a series of *Eulamia milberti* embryos of both sexes and near full term which were apparently perfect except for having the eyes on the lower side of the snout, almost in contact with one another and just posterior to the nostrils, and having no trace of an opening in the skin for the mouth, although the jaw cartilages were apparently normal. The specimens were preserved in formalin but dried out during the following years and were discarded. Again in 1946 similar embryos were collected, and about half a barrel were preserved; but all were lost in a hurricane which destroyed a dock building.

No abnormal young were found in the relatively large series of litters examined in 1948 and I had no later opportunity to see substantial numbers of *E. milberti* embryos. All litter mates exhibited the same abnormal condition and were remarkably uniform structurally. A very rough estimate of the frequency of occurrence is one set of abnormal young in 500 to 1,000 sets of apparently normal pups.

SEX RATIOS

It was the general observation that landings of adult *Eulamia milberti* at Salerno were in the ratio of 5 females to 1 male. A similar sex ratio was estimated for Salerno landings of *E. obscura* and for Bahama landings of adult *E. springeri*. A disproportionately large number of female *E. floridana* were landed at Salerno but the records do not furnish an adequate basis for an estimate. An insufficient number of *E. altima* or *E. springeri* were recorded for estimate. Murphy and Nichols (1916) say that the commonest large sharks in the waters about New York are the ground sharks *(Carcharhinus)*, and also that males of these fishes are rarely seen but toward midsummer many of the females enter our bays where they give birth to their young. They further state that the commonest ground shark is *Carcharhinus milberti*. The only record suggesting equality in the number of adults of the sexes of *E. milberti* is Captain Winkler's record of the capture of 26 males and 25 females off the Caribbean coasts of Nicaragua and Costa Rica in the fall.

Data on the sex ratio in young *E. milberti* is limited to a series of 203 young from 26 to 50 inches long collected by otter trawl in February 1958 off North Carolina. There were 91 males and 112 females in this collection.

Florida shark fishery records of carcharhinids other than those of the genus *Eulamia* show local segregation by sex and size but in no other carcharhinid nor in the hammerheads is there any clear indication from available records from Florida of great imbalance in the sex ratios of adults.

The unavailability of male *milberti* to baited hooks during the mating season may explain in part the smaller number of males in the landings. However, because Florida commercial shark fishing after 1946 was carried on out to depths greater than the maximum known depth range of the species, and because the males brought the fishermen a higher price than the females, it is certain that there was no intentional selection of females. The fishermen believed that the schools of males, if found, were easier to catch in large numbers. Females were far more abundant than males in the deeper water catches made off the Florida Keys in the late fall and early spring, and a much greater abundance of females characterized the winter catches on the west coast of Florida.

It has already been shown that approximately equal numbers of male and female *milberti* are born. The evidence that there are substantially more females than males in the adult population is very strong, if our information adequately covers the geographical range of the species. Although it is quite possible that segments of the adult population have been entirely overlooked in the offshore and midwater depths in the northern part of its range, the shortage of males in the population around southern Florida is remarkable.

There is some indirect evidence also of a shortage of males in the breeding population. If the females bear pups in alternate years, 50 percent of the adult females would be expected to be gravid in winter. I have previously reported (Springer, 1940) that only about 17 percent of the adult females taken in winter off Englewood, on the west coast of Florida, were gravid. I saw large numbers of *E. milberti* in 1942 and again from 1946 through 1949 at Salerno, and my notes include several estimates of the proportion of gravid to nongravid adult females seen on the dock. For the late-winter and early spring periods, it was estimated that substantially less than a third of the females were carrying pups. In my sample of 399 adult females taken for length-frequency data, approximately 18 percent were gravid.

Three interesting, if theoretical, explanations are suggested to account for the apparent differences in the number of males and females in *milberti* and in other *Eulamia*.

The mating pattern appears to be particularly dangerous to the males, since mating occurs when the females are in a feeding cycle while the males are not. That is, during courtship males may nip or slash to some extent but do not take large bites. The females have no such inhibitions except at the time the young are born, and fatal accidents to males may be frequent during courtship. However, if this explanation is to be acceptable, some further speculation is needed to suggest why *Galeocerdo* with a similar mating pattern is not represented in the adult population by a preponderance of females.

Geiser (1924) summarized a variety of reports on the higher death rate for males in some mammals, fishes, and invertebrates, and suggests that there is a genetic basis for this in certain cases where the possession of two sex chromosomes by the females * * * ensures a greater longevity of the female by "canceling out" possible mutations in the x-chromosome, especially associated lethals, while in the male there is no such "canceling out."

The third explanation is that the males occupy wider geographical and vertical ranges than the females, remain in the cooler parts of the ranges, and exhibit a greater tendency to wander than the females. Thus, greater numbers of males than females are lost to the breeding population by wandering and death in unfavorable environments.

Whatever the explanation for the unequal sex ratio, the smaller number of males is not a sufficient handicap to prevent *E. milberti* from being one of the commoner sharks.

GROWTH AND SIZE AT MATURITY

In Florida catches, adult male *Eulamia milberti* average 4.2 inches shorter than the average adult female and weigh 32 pounds less than the average nongravid adult female. The smaller size of the adult male is characteristic of all of the western North Atlantic carcharhinids although the size of males and females at birth is approximately the same. For about 20 years I maintained a close watch on landings of one or more commercial vessels and saw no *milberti* females longer than 92 inches and no males longer than 89 inches among the thousands that were examined.

The smallest sexually mature male in the material examined was 71 inches and the smallest sexually mature female was 72 inches in total length. Sexual maturity in the male is easily and positively determined because enlargement of the testes to functional size is immediately followed by the appearance of a ring of calcium at the surface of the major clasper cartilage. This ring is easily seen in cross section but since its effect is to stiffen the segments of the clasper, sectioning is unnecessary for positive determinations. Determination of sexual maturity in female specimens where the specimens were nongravid or had no courtship scars was made by examination of the ovary and the oviducts. The females were regarded as sexually immature if none of the eggs in the ovary had begun to increase in size and if the oviducts were smaller in diameter than is characteristic of the fully contracted oviducts in females following parturition. It may be noted in table 6 that, while at least 2 female *milberti* were mature at a length of 72 inches, 5 immature females of greater length were collected. Obviously the length at which the females may become sexually mature varies more than 4 inches.

The left skew of the length-frequency polygons shown in figure 5 may be the result of any of several variables including the length at which maturity is reached.

A total of 513 adult sandbar sharks was selected from southeastern Florida catches for measurement of total length and for comparison of

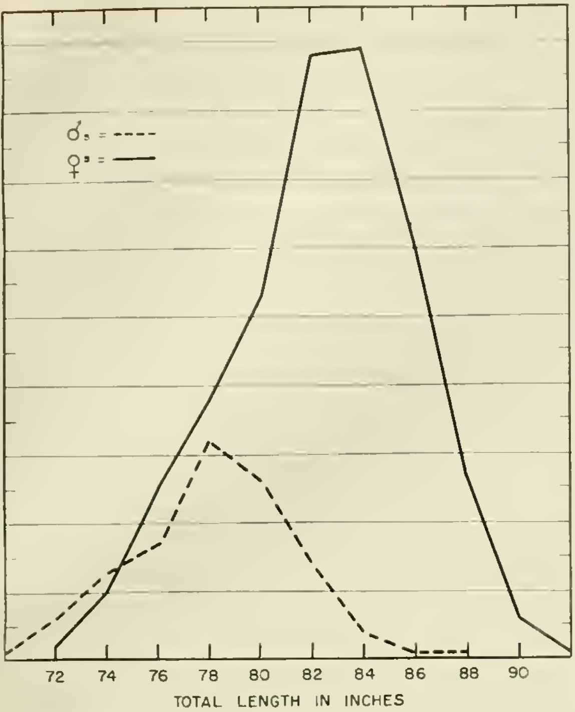

FIGURE 5.—Length-frequency polygons for adult male and female *Eulamia milberti* from southern Florida.

length frequency with the length frequencies of 76 sharks from off Fort Myers on the west coast of Florida and of 51 sharks from the Caribbean coast of southern Nicaragua and northern Costa Rica (table 6). To reduce bias, all sharks of all species in any catch were measured and recorded or none were recorded. Selection was affected by the scarcity of males. The comparatively large sample of fall females at Salerno had to be measured to get any catches that included males which rarely appeared there at that season. In the sample taken from the lower east coast of Florida, 10 sharks, 5 males and 5 females, were found to be immature. These immature sharks were excluded from the calculations of mean lengths of adults, but the sizes together with the dates of capture are given in footnotes to table 6, which shows the mean length of the sample lots.

By its migratory movements and its restriction to limited nursery areas, the North American population of *E. milberti* appears to be subject to constant mixing. It does not seem reasonable to expect a rigid segregation by area of origin of those *milberti* mating off southern Florida. This may be one factor in the apparent homogeneity of the population.

In some of the other carcharhinids, environmental or racial factors appear to affect the size at which the species becomes mature. For example, the average size of the bull shark, *Carcharhinus leucas*, from the vicinity of Trinidad is appreciably less than the average size of adults of the same species from the Gulf of Mexico. Important differences in the size at maturity as well as the size at birth separate the Texas and southern Florida populations of the little black-

TABLE 6.—*Mean length, number measured, and length range of adult* Eulamia milberti, *by sex, area, and season of eollection*

[Lengths in inches; length range in samples in parentheses]

Area	January-March		April-June		July-September		October-December		Combined data	
	Number in sample	Mean length	Number in sample	Mean length	Number in sample	Mean length	Number in sample	Mean length	Number in sample	Mean length
MALES:										
Southeastern Florida [1]	69	78.1 (71-89)	36	78.4 (72-86)	5	78.8 (76-82)	5	78.8 (73-82)	114	78.7 (71-89)
Southwestern Florida (from 2 schools)	29	79.0 (73-84)								
Nicaragua-Costa Rica					16	79.9 (72-89)	10	75.0 (71-84)	26	78.4 (71-89)
FEMALES:										
Southeastern Florida [2]	111	82.8 (72-91)	63	82.9 (76-92)	64	83.0 (74-91)	161	82.9 (73-90)	399	82.9 (72-92)
Gravid [3]									71	83.2 (73-88)
Gravid (from 1 school)							59	82.8 (75-88)		
Nongravid (from 1 school)							48	83.8 (75-87)		
Southwestern Florida: Nongravid	47	83.3 (72-90)								
Nicaragua-Costa Rica: Nongravid					7	82.6 (78-88)	18	83.9 (76-90)	25	83.5 (76-90)

[1] 5 immature males were collected with this sample but excluded from tabulation and from calculations of mean length: 1 specimen 64 inches long collected in March, 2 specimens each 66 inches long collected in August, 1 specimen 59 inches long collected in October, and 1 specimen 68 inches long collected in November.

[2] 5 immature females were collected with this sample but excluded from tabulation and from calculation of mean lengths: 1 specimen 72 inches long collected in January, 1 specimen 76 inches long collected in April, 1 specimen 73 inches long collected in July, and 2 specimens collected in October of which 1 was 75 inches long and the other 76 inches.

[3] From preceding collections.

tip shark, *Carcharhinus limbatus*, but whether different species, subspecies, or races are involved remains to be determined.

In the last week of February 1958, I was able to get evidence that the edge of the Continental Shelf off the Carolinas is indeed an important wintering ground for immature *milberti*. A series of 25 tows with a modified Number 41 otter trawl made by the Bureau of Commercial Fisheries exploratory vessel *Delaware* while I was aboard took 203 immature *milberti* between the offings of Cape Hatteras and Cape Lookout. In one tow in 52 fathoms, 197 *milberti* from 27 to 43 inches long were taken and in three other tows at depths of about 50 fathoms 4 *milberti* were picked up. Tows made at other depths from 20 to 250 fathoms failed to catch *milberti*. The water temperature at the bottom at this time was about 64° F. in 50 fathoms, but temperatures were appreciably cooler, about 57° F., in both 30 fathoms and 80 fathoms.

It is suggested that the 197 young *milberti* taken in February 1958, were young of the year, born in the summer or early fall of 1957, and that their average length of 34 inches represented growth from birth of about 12 inches in approximately 7 months. However, if it is correct that all of these young were born in 1957, some may have grown as little as 5 inches and some more than 20 inches. Such an irregular growth pattern would help to explain some other facts of the *milberti* life history, for example, the seasonal differences in the vitamin-A potency of adults taken by the shark fishery.

In January and February 1945, I obtained two boatloads of sharks from O. E. Holley, an expert shark fisherman at Fort Myers, Fla. Of the 133 sharks brought in, 73 were adult *E. milberti* and none of the female *E. milberti* were gravid. The 27 males in the sample ranged from 74 to 84 inches in total length (average, 79 inches) and weighed from 94 to 130 pounds (average, 113.7 pounds). The 46 females ranged from 72 to 90 inches in length (average, 82.3 inches) and weighed from 102 to 184 pounds (average, 145.1 pounds). The specimens were weighed and measured about 36 hours after capture and the stomachs of all of the sharks were empty or nearly empty. Weight among sharks of the same length varied considerably. Thus, three 78-inch males weighed 94, 115, and 122 pounds, while eight 83-inch females weighed 122, 127, 141, 142, 146, 148, 161, and 162 pounds, and six 78-inch females weighed 102, 136, 147, 147, 154, and 164 pounds. Weights of livers, other viscera, fins, and eviscerated carcasses were obtained, but unfortunately when these weights were recorded they were tied in solely with the total weight of each shark. Analysis of the figures gives some indication that liver weights in female *E. milberti* contributed disproportionately to total weights. Livers of males weighed from 7 to 14 pounds and livers of females from 7.25 to 31 pounds. The average weight of 40 livers from females was 18.5 pounds.

It would be convenient and would fit most of the facts to assume that the growth of *Eulamia milberti* is very rapid, but there is merely presumptive evidence for this. It is by no means the only view that could be reasonably advanced and it would be especially weak for *milberti* for which the immature part of the population is not well known. Nevertheless, on the basis of little real evidence I suggest that it is probable that growth from birth to maturity takes about 2 years, occasionally 1 year, rarely 3 years.

The length uniformity indicated in table 3 for both male and female adult *milberti* from different seasons would be expected from a species with determinate growth. Predictable adult size in relatively narrow ranges also characterizes other species of *Eulamia*, *Negaprion*, and perhaps *Carcharhinus*. On the other hand, it is presumed that some individuals of *Prionace* and *Pterolamiops* continue growing after maturity to reach abnormally large sizes. Records of *Galeocerdo* more than 14 feet long are not uncommon in the literature and some of these records apparently are reliable and I accept them as such. Nevertheless, I have seen more than a thousand large *Galeocerdo* from the Florida–West Indian region and have measured all of the exceptionally large ones that I have seen. None were found to exceed 14 feet in total length. Great increase beyond the usual adult size has been noted, however, for *Sphyrna* sp., the great hammerhead. In my sample of 52 adult females, 5 were much larger than would be expected. If, as indicated by my sample, the usual size for adult female great hammerheads is 10 to 12 feet, the attainment of approximately 15 feet by 10 percent of the lot precludes description of the growth as determinate, at least for the great hammerhead. One individual, measured but not included in the sample, was 18 feet long. Although the continuation of growth after maturity as a peculiarity of the female apparently does not obtain in *E. milberti*, it is evidently the pattern in some species of *Sphyrna*, in *Pterolamiops*, and occasionally in *Galeocerdo*.

FOOD AND FEEDING HABITS

Examination of stomachs of *Eulamia milberti* as a source of information on the food of the species has been disappointing. Comparison of the feeding habits of *E. milberti* with the feeding habits of other carcharhinid species of the Florida region, however, has proved to be more illuminating. Various bits of evidence show that *E. milberti* is a discriminating feeder; that it is a bottom feeder; that it feeds on small bottom fish and invertebrates rather than the larger ones; that it prefers fresh fish to stale or decomposed fish; that it prefers fish to porpoise meat or to the flesh of domestic animals; and that its feeding is remarkably successful in comparison with some of its larger carcharhinid relatives.

A very large proportion of the sharks in commercial landings were found to have empty stomachs. An obvious explanation for this is that most of the sharks were examined after the passage of several hours when small and readily digestible meals would presumably have been completely hydrolized. Observations and examinations of stomachs of sharks of many species has led me to the opinion that the larger species find food less often than the small ones, and that through no choice of their own, large sharks have empty stomachs more often than not.

In the stomachs of *Eulamia milberti* a few fish remains, usually not identifiable as to species, cephalopods, and crustacean remains were found from time to time. Goatfishes (Mullidae), snake eels (Ophichthyidae), sea robins (Triglidae), and cusk eels (Ophidiidae), were among the types most commonly found. A collection of 167 *milberti*, all with fish, octopus, or crabs in their stomachs was reported in an earlier publication (Springer, 1946). There were unusual circumstances about this catch, however, which suggest that the large amount of food in the stomachs resulted from the sharks being taken in an area of localized upwelling that had stunned large numbers of fish and bottom invertebrates. Very few instances were noted in which shark remains were found in *milberti* stomachs and no evidence was found that *milberti* commonly fed on large turtles, porpoises, birds, ships' garbage, or surface material recognized by the inclusion of Sargassum weed or typical surface-dwelling forms.

Some indication of the probable food preferences of *E. milberti* can be found in the experiences of commercial fishermen. It was demonstrated to the satisfaction of Florida shark fishermen that there were somewhat different requirements for bait depending on what species was sought. It was also found that the increased cost of very fresh bait, or bait frozen when fresh, was fully justified by the improved catches. All of the carcharhinid species of the Florida area, even those frequently feeding on garbage, apparently prefer fresh bait. The bait most universally accepted by all species was fresh fish and *E. milberti* rarely was taken on any other bait. Some species, notably *Eulamia obscura* and *Galeocerdo*, took cut porpoise readily, and one species, *Carcharhinus leucas*, occasionally preferred pieces of fresh shark. Cut bait was found to be very much better than the entire fish of any species. Probably the diffusion of juices from cut bait was greater than from fish in the round.

In the Salerno, Fla., area the best catches were obtained by sets made in the late afternoon with pickup of the lines starting the following morning as soon as there was sufficient light to locate the buoys. The freshness of the bait may have had some bearing on the apparent better fishing at dusk and during the early part of the night. Catches made during the early morning and throughout the day were not infrequent, however, and it seems probable that the early part of the night is merely a period of increased feeding activity for *Eulamia milberti*.

It is the common habit of many species of sharks, including *Eulamia milberti*, to nudge or hit objects with their noses. I am convinced that they do this to test the object for juices. The edible qualities of the object are thus determined by the shark through sensory crypts which are widely dispersed over the skin of the head and body. These organs, which perform a function corresponding to taste, have been described in detail by Budker (1938). Under ordinary circumstances the testing procedure is routine for objects which are not moving or which are not part of a series of similar-appearing objects, one of which has already proved edible. The procedure may be omitted if there is competition for food.

It seems improbable that the sensory crypts of the head function in any other way than as gustatory organs. To find suitable food or to find an area having food in it, *Eulamia milberti* as well as many other species depends on olfactory organs. Experiments by Parker and Sheldon (1913) with *Mustelus canis* probably outline the general pattern of behavior of the cacharhinids in their search for food.

Carcharhinid sharks in general are opportunists in feeding and necessarily so. Without special techniques, developed in some species but not to my knowledge in *Eulamia milberti*, sharks are relatively ineffective at catching uninjured fish in open water or even at finding such slow-moving objects as crabs. The shark's ability to exist on a regimen of feast and famine, imposed by its ineptness in catching food at will, is probably made possible through its unique digestive and fat-storage organs. A general outline of the processes of digestion and fat storage by sharks is beyond the scope of this report. It is pertinent to point out that their digestion is rapid and thorough, and that the shark's liver with its high percentage of oil is a good index of its metabolic well-being. The larger, fatter livers are found in sharks in good condition while small livers with little oil are frequently found in sharks having severe injuries, sharks in obviously poor condition, or in the males at the end of the mating season.

The liver of adult *E. milberti* typically represents between 10 and 15 percent of the animal's total weight, rarely more than 18 percent and rarely less than 6 percent. The proportional weight of the liver in adult *E. milberti* males is lower than in females, but the liver weight of the species is remarkably uniform in comparison with larger species of carcharhinids within its geographical range. This is strong evidence that *E. milberti* is successful in getting an adequate supply of food regularly. *Galeocerdo cuvier*, *Carcharhinus leucas*, and *Eulamia obscura*, all species more than twice as heavy as *milberti*, frequently have livers 25 percent or more of the total weight of the fish. On the other hand, they often have very small livers, as low as 3 percent of the total weight. The inference is reasonable that the larger species have greater difficulties finding food, or more precisely, may have to wait longer between meals. This inference from liver weight also is consistent with the observation that the foods of the larger species are frequently of a less digestible type and may be taken as a kind of desperation measure and certainly not as a first choice. *Galeocerdo*, for example, frequently fills its stomach with large horseshoe crabs, huge horse conchs complete with shell, or even old shoes and tin cans.

Because of commercial interest in the vitamin-A content of shark-liver oils that existed for a number of years, a large amount of data is to be found in the literature on the subject. Also available to me are data on the oil and vitamin-A content of livers of *E. milberti* taken at Salerno. Some determinations for Salerno species were given in an earlier publication (Springer and French, 1944). Better methods of estimation of the vitamin-A concentration in liver oils came into general use later, but these did not appreciably alter the general trends observed.

The tendency in each species to an increase in the vitamin-A concentration, or potency, of the liver oil with the increase in size of that species has been noted by many workers (Pugsley, 1939; Brocklesby, 1941; Templeman, 1944; Ripley and Bolomey, 1946, et cetera). The liver-oil vitamin-A potency varies considerably. Each species and locality produces sharks having potencies that are approximately predictable. Characteristically, in most species the males produce oil of somewhat higher vitamin-A potency than that of the females, but they often have less oil in their livers.

An hypothesis which has general support is again advanced here that within a given species and locality, the total amount of vitamin A in the liver of a shark is roughly proportional to the age of the shark. Thus, the older the shark the greater is the total amount of vitamin A in its liver. The rate of increase in vitamin A may rise sharply as the shark becomes sexually mature but this does not affect the general trend in the total amount of vitamin A stored. Fluctuations in the amounts of oil stored in the liver may normally accompany such events as young bearing, mating, and periods of poor feeding, and these fluctuations apparently affect potency, but the total amount of vitamin A is subject to fluctuation to a lesser degree. It has been shown for *Galeorhinus zyopterus* of the Pacific coast (Ripley and Bolomey, 1946) that the total amount of vitamin A in the largest males and largest females does not greatly differ.

Livers of *Squalus suckleyi* of the Pacific coast have a higher average vitamin-A potency than livers of *Squalus acanthias* of the Atlantic. The two species are morphologically so similar that taxonomists have had doubts about their separation. Concerning the differences in liver oil potency, Templeman (1944) has the following comment:

> Whether the greater length of the mature *Squalus sucklii* reflects a greater age or a greater growth rate than those of *Squalus acanthias* is not known, but this greater size is possibly partly responsiblé for the higher vitamin-A value of its liver oil.

The greater vitamin-A content of shark livers does not always occur in the larger individuals in a given species. For example, my own measurements and assays show that *C. leucas* off the mouth of the Mississippi River average appreciably longer and heavier than *C. leucas* taken off the mouth of the Orinoco River; but the liver-oil potency of the species from the vicinity of the Mississippi River mouth is extremely low, while that of the *C. leucas* from the vicinity of the Orinoco is high. These differences are quite great and reasonably constant. Adult male *C. leucas* from the Orinoco area have liver-oil potencies above 50,000 I.U./gm. (international units per gram uncorrected for irrelevant absorption), while adult males from the Mississippi area generally have liver-oil potencies of 1,000 to 5,000 I.U./gm. Variation in liver-oil potency by area is perhaps greater in *C. leucas* than in most shark species of the northwestern Atlantic, but the variation is appreciable in all species.

A rough classification by regions of part of the northwestern Atlantic on the basis of shark-liver vitamin-A potency from data assembled by the shark fishery is as follows:

Extremely low potencies—Gulf of Mexico; low potencies—northern Bahamas and shallow-water areas of the West Indies; intermediate potencies—Carolina coast, east coast of Florida, and coast of Cuba; high potencies—southern Caribbean, coast of Costa Rica to the Guiana coasts. To a limited extent this classification is useful to trace probable origins of elements of migratory stocks. Potency differences among liver oils taken from single adult specimens of *Eulamia milberti* were in the range from about 2,500 to 25,000 I.U./gm. One exception was noted in that one assay (the only one available) on mixed *E. milberti* livers from the coast of Nicaragua–Costa Rica was substantially higher, about 38,000 I.U./gm.

If *E. milberti* from the coast of Nicaragua–Costa Rica returned regularly to the species' Atlantic population center from Florida northward, some among the hundreds of livers of *milberti* taken at Salerno, and assayed separately should have had potencies greater than 38,000 I.U./gm. None had such a high potency.

The average potency of oil from livers of *Eulamia milberti* was found to be substantially lower from the southwest coast of Florida than from the southeast coast although the extremes in individual potencies were about the same. Since both stocks have a common origin from the Atlantic coast north of Cape Canaveral we might assume that the difference in averages results from either the lower age of the adult *milberti* reaching the west coast of Florida or a lower rate of vitamin-A accumulation due to the period spent in the Gulf of Mexico, or from both of these.

The liver-oil potency of the eight adult female *E. milberti* from the mouth of the Mississippi River was higher and the total vitamin A from these sharks was about the amount to be expected from similar sharks taken on the east coast of Florida. This potency would be expected only if these sharks originate outside of the Gulf of Mexico.

To the extent that data on vitamin-A potency determinations have any validity for the determination of age or the areas of origin of migratory stocks, they support the general conclusions that *E. milberti* does not live to a great age and that those individuals migrating a great distance to the coast of Nicaragua–Costa Rica do not return. .

ABUNDANCE

The inshore range of the sandbar shark has made this species readily available to the shark fishery. This was particularly noticeable at Salerno, where the range is restricted by a narrowing of the Continental Shelf and where special conditions of current and temperature tend to produce a narrow path inshore for the southbound migrants. Approximately 58 percent of the sharks landed by the fishery at Salerno between 1938 and 1946 were sandbar sharks. Although present throughout the year, they were comparatively more frequent in Salerno catches from December through July as shown by records of the catch per unit of effort (Springer, 1951). Except for winter fishing on the southwest coast of Florida which produced a few hundred *E. milberti* each winter, few sandbar sharks were taken in the Gulf of Mexico.

It is estimated that during the period 1935 to 1950 from 5,000 to 15,000 sandbar sharks were taken yearly from the entire range of the fishery and that these were nearly all adults with an average weight of about 130 pounds. The yearly catch might be estimated, therefore, as between 650,000 and 1,950,000 pounds, a small quantity compared with yearly landings by the commercial fishery of many species of bony fishes. During the years that the shark fishery operated, it was prosecuted vigorously, and, although there was no evidence that fishing pressure reduced the stock of sandbar sharks, it was found that the catch per unit of effort was reduced by concentrating too much gear in one area. Efforts to expand production were successful chiefly by extension of the area of fishing into the ranges of other species of sharks. A fluctuation in abundance with a low in every third year was found in the catch per unit of effort at Salerno (Springer, 1951).

Although data are lacking to support such a contention except observations at sea, it is estimated that several other species of *Eulamia*, particularly *E. floridana*, occur in substantially greater species-mass around Florida than does *E. milberti*, chiefly because of the greater area of their habitats.

It is generally recognized that marine animal populations are unstable and are subject to remarkable changes in total numbers and occasional shifts in geographical range. Such changes may, of course, occur in the Atlantic population of *E. milberti*.

A concentration of *E. milberti* appeared for a few days in the late spring or early summer of 1935 off Dog Keys Pass on the coast of Mississippi. These sharks were not only out of their normal range but behaved in a way that is not normal for *milberti* or perhaps for any shark. They struck at anything thrown into the water, fought one another over pieces of charcoal, fought so vigorously that some were killed and eaten by others of the school. Sharks frequently follow shrimp boats such as we were using at the time, and churn the surface of the water after scrap fish thrown overboard; but the intensity of this attack by out-of-range *milberti* was much stronger than any shark action I have seen since.

Although no great fluctuations were noted in the general abundance of *E. milberti* during the period from 1935 to 1950, its competitor, the bull shark *C. leucas*, appeared once to go through a major but temporary shift in abundance. In 1937 so many bull sharks were caught off Salerno that catches exceeded the demand. The company buying shark livers and oil was forced to delay payments to fishermen for a period of several months. This was not merely a matter of economic adjustment to be settled by a reduction in price but the supply of tanks and drums for storage of liver oil was exhausted and a court injunction was finally issued to stop all shark landings because shark carcasses were accumulating along the shores. This was the only known appearance of bull sharks in large numbers on the east coast of Florida. It seems likely that persistence of great numbers of bull sharks, especially north of Cape Canaveral, would have adversely affected the population of *E. milberti*.

ENEMIES

The principal predators on sharks are other sharks of larger size. Wherever concentrations of mixed sizes occur predation by the larger sharks on the smaller ones is normal. The concentration of sharks occurring near the mouth of the Mississippi River in the summer months may be as great as anywhere in the world. Some idea of the predation that may occur is furnished by the results of one line of 180 shark hooks set on the night of July 22, 1947, off Pass a l'Outre, La. This line caught 68 large sharks, whole and undamaged, but 40 of the hooks had only the heads of large sharks and 12 more had only the heads of small sharks. Almost all of the larger sharks on the line contained small sharks or pieces of large ones. One tiger shark, *Galeocerdo*, had swallowed a medium-sized bull shark which in turn had a major portion of a somewhat smaller blacktip in its stomach. The blacktip, however, had driven the head of a *Mustelus canis* about 4 feet long up the leader so it would be reasonable to assume that the large tiger shark was the fourth shark to be taken in that one night on one hook. The bottom conditions, depths, and temperatures where this line was set appeared to be similar to conditions on *milberti* nursery grounds but predation would presumably eliminate young *milberti* in the area.

Full-grown sandbar sharks probably are rarely subject to successful shark attack by other species. The tiger shark (*Galeocerdo*), dusky shark (*Eulamia obscura*), and bull shark (*Carcharhinus leucas*), have all been found occasionally with pieces of full-grown sandbar shark in their stomachs, but the sandbar sharks may have been on shark lines when attacked. Perhaps none of these species are able to catch adult sandbar sharks under ordinary circumstances. Great white sharks, *Carcharodon carcharias*, have been found with adult *milberti* in their stomachs and it is probable that the great white shark could catch them. The white shark is not common enough, however, to be an important factor in predation. At Salerno, captures were about 27 great white sharks per 100,000 of all species.

All carcharhinids more than 6 feet long may occasionally eat young *E. milberti*, but circumstances of seasonal and geographical distribution keep most species from preying on them. There are two notable exceptions: the tiger shark and the bull shark. These sharks feed on young sharks or on small species regularly, and both may be found at times within the known range of young *milberti*.

Tiger sharks, perhaps for reasons of poor speed and maneuverability associated with their smaller and lighter weight fins, catch young sharks less frequently than do bull sharks. Furthermore, tiger sharks are primarily nocturnal in forays into inshore waters and at such times newborn or small sharks retreat to shoaler water. On the other hand, bull sharks are not exclusively nocturnal and they are more frequent in relatively shallow water. Stomach contents show that they are regularly predatory on small species such as *Carcharhinus acronotus*, *C. porosus*, *Scoliodon terra-novae*, and *Aprionodon isodon*. The bull shark also is the only species in the range of *E. milberti* with a preference for shark as a bait.

There is strong circumstantial evidence, derived from an examination of the geographical ranges and nursery-ground preferences of the various species of *Eulamia*, that the bull shark is the most important predator on young sharks and actually restricts the distribution of *milberti*. The life history of the bull shark is similar to that of species of *Eulamia*, but the bull shark is always found in shallow water and its nursery grounds are in bays or estuaries, even in brackish and fresh water. The nursery range of the bull shark is shoaler and less saline than the nursery range of *milberti*, but adult bull sharks inhabit the depth and salinity range normal to nursery grounds of *milberti*. Young bull sharks remain in estuarine waters during the early growing season, and since the females do not eat at the time the young are born and generally move out of the very shallow water immediately after the birth of the young, the young bull sharks are protected to some degree from predation by the large members of their own species.

Bull sharks occur from Long Island southward and are migratory but their centers of abundance are in the Gulf of Mexico and southward, particularly near the mouths of large rivers. Along the Atlantic coast north of Florida, bull sharks are not common, but may be subject in this area to great fluctuation in abundance. Bull sharks are extremely common around the mouths of the Mississippi and Orinoco Rivers and between these points along the inshore Continental Shelf. There is practically no information about their occurrence in the West Indies.

No *Eulamia* except *milberti* is known to have nursery grounds within the geographical and habitat range of the bull shark. The nursery ranges of *E. altima* and *E. obscura* are well offshore in deeper water, *E. floridana* nursery grounds are on offshore banks where bull sharks do not go, and bull sharks are uncommon at least, or normally absent around reefs which are nursery grounds for *springeri*. The suggestion is advanced here that predation by the bull shark is the chief reason, and perhaps the only reason, for the scarcity of *E. milberti* in the Gulf of Mexico and southward in continental waters. The comparatively few bull sharks of the Atlantic coast may be presumed to act as a check on the numbers of young *E. milberti*, but without disastrous effects for that species.

Some interesting complications are associated with predation of large sharks upon smaller ones. Evidently all carcharhinid sharks will eat other sharks sometimes if not regularly. However, it is a shark fisherman's axiom that sharks left on the line to spoil will burn out the fishing grounds and make it necessary to move away 5 miles or so to continue fishing. A rationale has been partly outlined in an earlier publication (Springer, 1954) covering experiments with *Mustelus* in tanks. Feeding of *Mustelus* was entirely inhibited in the presence of shark flesh that had been allowed to stand at room temperature for 4 days.

Presumably sharks have no difficulty digesting shark flesh provided it is fresh. Although sharks appear to be able to digest the partially decomposed flesh of other vertebrates, their digestive processes are slowed or stopped completely when they swallow large quantities of decomposing sharks or rays.

The flesh of sharks becomes strongly alkaline during decomposition. The continuous liberation of ammonia through action of enzymes produced during the course of ordinary putrefactive decomposition on the urea that normally occurs in sharks (see Smith, 1936), seems effectively to block, or at least to greatly retard, digestion. The proteolytic enzymes of the shark's stomach are most active in an acid medium (Sprissler, 1942). In my examinations of juices of shark stomachs in the field, estimates were made of the hydrogen-ion concentration, as shown by indicator solutions. Juices from shark stomachs that contained large amounts of shark flesh in obviously decomposing condition were found to be substantially above pH 8.0, whereas juices from shark stomachs containing fish, turtles, birds, or small amounts of fresh shark were estimated at pH 4.0 or below. It is not clear whether excessively large meals of decomposed shark flesh produce any result more serious than delayed digestion.

I have not seen evidence that internal parasites ever greatly damage *Eulamia milberti*. Roundworms in the stomach, roundworms and adult tapeworms in the scroll-type intestine, and copepods on the gills and external surfaces were commonly seen. In comparison with other large Florida sharks, *milberti* seemed to be the least troubled by parasites. Occasionally, sharks taken from lines apparently set in areas of extraordinary abundance of a small isopod were found to have a large proportion of the viscera eaten away by swarms of the isopods, which had entered the body cavity by way of the soft parts around the anus. It has been assumed that these isopods attack successfully only after the sharks die on the lines or at least have been restricted in movement. Similar isopods attack living small fishes and man (Springer, 1957) and it seems quite possible that they may also attack living sharks. If they successfully attack living sharks they may be one of the principal enemies of sharks in temperate and tropical waters of shallow and moderate depth. I have seen evidence of their work on shark catches made off South Carolina, Florida, Louisiana, Cuba, and southern California.

SUMMARY

The overlapping geographical and habitat ranges and superficial resemblance of *Eulamia milberti*, the sandbar shark, and *Carcharhinus leucas*, the bull shark, have led to some confusion and a tangled nomenclature. The recognition of *milberti* of Müller and Henle as the species name for the sandbar shark is based on the opinion that *plumbeus* of Nardo is a *nomen nudem*.

The sandbar shark differs from the bull shark in the structure and spacing of the dermal denticles, in having a ridge in the skin of the back between the first and second dorsal fins, and in the smaller size and less robust body form. The sandbar shark swimming in the open sea or in an exhibition tank may be distinguished readily from the bull shark because of its comparatively more erect and higher first dorsal fin placed slightly further forward, its somewhat larger eye, its somewhat longer snout, and its generally less robust body form.

Although the sandbar shark inhabits both the eastern and western parts of the Atlantic, this report concerns only one population of the species centered along the southeastern coast of the United States.

Species of the genus *Eulamia* usually are sharks of the continental shelves, oceanic banks, and island terraces throughout their life cycles in contrast to most species of *Carcharhinus*, which are typically shallow-water forms having their nursery grounds in brackish or fresh-water estuaries, river mouths, or along continental beaches, or in island lagoons. *Eulamia milberti* occupies the shoalest habitat range of the 5 or 6 species of *Eulamia* of the Atlantic coast of North America and enters estuaries to some extent to give birth to its young. Its habitat preference may thus be said to be intermediate between that typical of *Eulamia* and that typical of *Carcharhinus*.

The sandbar shark is clearly separable from all other species within its geographical range and exhibits little variation in form and in tooth count.

The sandbar shark, *Eulamia milberti*, is found in waters of suitable depth, southward from Cape Cod along the Atlantic coast. It occurs in the Gulf of Mexico and along the Caribbean coast of Central America to Costa Rica. It occurs casually off the northern coast of Cuba and along the western edges of the Bahama Bank, but principal elements of the population are confined to the western side of the Gulf Stream. Sandbar sharks occur as bottom dwellers out to depths of 100 fathoms (extreme record 135 fathoms) and may occasionally move out in midwater to oceanic situations. The principal part of the range of adults, away from the nursery grounds, has been shown by commercial catches to be in depths of 10 to 30 fathoms.

The sandbar shark populations of the northern and western parts of the Gulf of Mexico and the Caribbean coast of Central America are small and are probably not self-sustaining without recruitment from the main population by migratory wandering or failure of such orientation mechanisms as the species may possess.

The primary nursery range lies in shallow coastal waters of less than 20 fathoms from Cape Cod, Mass., to Cape Canaveral, Fla.; and a secondary nursery range lies in the Gulf of Mexico west of Mobile Bay and north of the 28th parallel. Newborn sandbar sharks are not known outside the general geographical limits of the nursery ranges, but the young sharks move offshore to deeper (and warmer) water during the winter.

The species is migratory with annual movements of some segments of the population extending at least 600 miles. Sandbar sharks in migratory passage around the southern tip of Florida hold to depths of 50 fathoms or more in apparent avoidance of coral reef areas. Their vertical distribution in the southern part of the species' geographical range, however, is somewhat deeper than in the northern part, suggesting thermal influence in the selection of habitat.

There is reason to believe that female sandbar sharks are inhibited from feeding at the time of birth of the young and for a short time thereafter. Nursery grounds are away from the normal range of the males thus giving additional protection to newborn young. Feeding appears to be inhibited in male sandbar sharks during periods of active courtship.

Young of nearly uniform size, numbering from 1 to 14 in each litter, are born in early summer (probably also in late spring) off northern Florida. The average number in a litter is 9 and the modal number 10. The gestation period is from 8 to 12 months' duration, with 9 months estimated in the latitude of northern Florida. Both oviducts are functional, a single embryo develops in each shell membrane, and a pseudoplacenta with a simple stalk (yolk-sac attachment) forms.

Length at birth is approximately 24 to 25 inches in the latitude of northern Florida but may be less in higher latitudes. Young born in the vicinity of Long Island, N. Y., have been reported to be 22 to 23 inches long at birth, and even smaller young have been reported from Chesapeake Bay.

Although approximately equal numbers of males and females are born, catches indicate a much larger proportion of adult females than adult males except off the coast of Nicaragua.

Females produce young no oftener than every other year, but since only about 18 percent of the adult females taken in the fishery were found to be gravid, this apparent low productivity may be the result of the low proportion of males in the adult population.

In samples from Florida, adult males are from 71 to 89 inches in total length and adult females from 72 to 92 inches. Average weights of adults in samples from southern Florida are for males, 114 pounds, and for nongravid females, 145 pounds.

The mean length and length-frequency distribution (size range) by sex in catches believed to have been made from single large schools closely approximated the mean length and size range by sex of all adults of the species from southern Florida. No appreciable difference was noted in mean lengths and size ranges of adults in samples taken at various seasons on the east coast of Florida, the west coast of Florida, and the Caribbean coast of Nicaragua and Costa Rica except the constant difference of about 4.2 inches between average lengths of adult males and adult females. Differences in the average lengths of gravid and nongravid females were small.

The rate of growth is not known. Indirect evidence indicates that it may be very rapid until sexual maturity is reached, after which little growth occurs.

The sandbar shark feeds chiefly on small bottom-dwelling fishes, mollusks, and crustaceans. It rarely swallows indigestible materials. Uniformly plump livers suggest that *milberti* has little difficulty in meeting its requirements for food.

From commercial catches it is estimated that the population is small in species mass as compared with many teleosts.

The only important predators on sharks are other sharks and not necessarily sharks of other species. Full-grown sandbar sharks, unless injured or caught on a shark line, appear rarely to be eaten by other sharks. Young sandbar sharks are especially vulnerable to attack by large sharks, particularly by bull sharks, but also to a lesser extent by tiger sharks, dusky sharks, and full-grown sharks of their own species.

LITERATURE CITED

Backus, Richard H.

1957. Notes on western North Atlantic sharks. Copeia, No. 3, pp. 246–248.

Backus, Richard H., Stewart Springer, and Edgar L. Arnold, Jr.

1956. A contribution to the natural history of the white-tip shark, *Pterolamiops longimanus* (Poey). Deep-Sea Research, vol. 3, pp. 178–188.

Beebe, William, and John TeeVan.

1928. The fishes of Port au Prince Bay, Haiti. Zoologica, vol. 10, No. 1, pp. 1–279.

Bigelow, Henry B., and William C. Schroeder.

1948. Sharks. *In* Fishes of the western North Atlantic. Memoir No. 1, Sears Foundation Marine Research, pt. 1, pp. 59–576.

1953. Fishes of the Gulf of Maine. U.S. Fish and Wildlife Service, Fishery Bulletin 74, vol. 53, pp. 1–577.

Brocklesby, H. N.

1941. The chemistry and technology of marine animal oils with particular reference to those of Canada. Fisheries Research Board of Canada, Bull. 59, pp. 1–442.

Budker, Paul.

1938. Les cryptes sensorielles et les denticules cutanés des Plagiostomes. Annales de l'Institut Océanographique, vol. 18, pp. 207–288, pl. 1.

Bullis, Harvey R., Jr.

1955. Preliminary report on exploratory longline fishing for tuna in the Gulf of Mexico and the Caribbean Sea. Commercial Fisheries Review, vol. 17, No. 10, pp. 1–15.

Cadenat, John.

1950. Rapport sur les Sélaciens des côtes du Sénégal et plus spécialement sur les Requins. Bulletin de l'Institut français d'Afrique noire, vol. 12, pp. 944–975.

1957. Notes d'ichtyologie ouest-africaine. XVII Biologie. Régime alimentaire. Bulletin de l'Institut français d'Afrique noire, vol. 19, ser. A, No. 1, pp. 274–294.

Captiva, Francis J.

1955. Longline gear used in yellowfin tuna exploration. Commercial Fisheries Review, vol. 17, No. 10, pp. 16–20.

Cowles, Raymond B.

1945. Temperature induced sterility and evolution. Science, vol. 101, No. 2618, pp. 221–222.

Evermann, Barton W., and Millard C. Marsh.

1902. The fishes of Puerto Rico. Bulletin of the U.S. Fish Commission, vol. 20 (1900), pt. 1, pp. 51–350, pls. 1–51.

Ford, E.

1921. A contribution to our knowledge of the life histories of dogfishes landed at Plymouth. Journal of the Marine Biological Association of the United Kingdom, New Series, vol. 12, No. 3, pp. 468–505.

Fowler, Henry W.

1936. The marine fishes of west Africa. Bull. American Museum National History, vol. 70, pt. 1, pp. 1–605.

Garman, Samuel.

1913. The Plagiostomia (sharks, skates, and rays). Memoir Museum Comparative Zoology, vol. 36, pp. 1–518, pl. 1–77.

Geiser, Samuel Wood.

1924. Differential death-rate of the sexes among animals, with a suggested explanation. Washington University Studies, Science Series, vol. 12, No. 1, pp. 73–96.

Gill, Theodore N.

1862. Analytical synopsis of the order Squali. Annals Lyceum Natural History, New York, vol. 7, pp. 367–408.

Hickling, C. F.

1930. A contribution towards the life-history of the spur-dog. Journal of the Marine Biological Association of the United Kingdom, new series, vol. 16, No. 2, pp. 529–576.

Hildebrand, Henry H.

1954. Shrimp (*Penaeus aztecus* Ives) grounds in the western Gulf of Mexico. Publication of the Institute of Marine Science University of Texas, vol. 3, No 2, pp. 233–366.

Hildebrand, Samuel F., and William C. Schroeder.

1928. Fishes of Chesapeake Bay. Bulletin of the U.S. Bureau of Fisheries, vol. 43, pt. 1, pp. 1–366.

Leigh–Sharpe, W. Harold.

1920. The comparative morphology of the secondary sexual characters of elasmobranch fishes. Memoir I. Journal of Morphology, vol. 34, No. 2, pp. 245–265.

1921. *Idem*, Memoir II. *Ibid.*, vol. 35, No. 2, pp. 359–380.

1924. *Idem*, Memoir VI. *Ibid.*, vol. 39, No. 2, pp. 553–566.

Meek, Seth E., and Samuel F. Hildebrand.

1923. The marine fishes of Panama. Field Museum Natural History Publication No. 215, Zoological Series, vol. 15, pt. 1, pp. 1–330.

Müller, Johannes, and F. G. J. Henle.

1841. Systematische beschreibung der plagiostomen. Berlin, pp. 3–200, pls. 1–60.

Murphy, Robert Cushman, and John Treadwell Nichols.

1916. The shark situation in the waters about New York. Brooklyn Museum Science Quarterly, vol. 3, No. 4, pp. 145–160.

Nardo, G. D.

1827. Prodromus Observationum et disquisitionum Adriaticae Ichthyologiae. Giornale fisica, chimica, storia naturale, medicina ed arti, vol. 10, pp. 22–40. Pavia (1827).

Nichols, John Treadwell.

1918. Ground sharks of Florida and elsewhere. [Abstract.] Copeia, No. 53, p. 13.

1929. The fishes of Puerto Rico and the Virgin Islands. New York Academy of Science Survey, vol. 10, Pt. 2, pp. 161–295.

Nichols, John Treadwell, and Charles M. Breder, Jr.

1927. The marine fishes of New York and southern New England. Zoologica, vol. 9, No. 1, pp. 1–192.

Olsen, A. M.

1954. The biology, migration, and growth rate of the school shark, *Galeorhinus australis* (Macleay) (Carcharhanidae) in south-eastern Australian waters. Australian Journal of Marine and Freshwater Research, vol. 5, No. 3, pp. 353–410.

Parker, G. H., and R. E. Sheldon.

1913. The sense of smell in fishes. Bulletin of the U.S. Bureau of Fisheries, vol. 32, Doc. No. 775, pp. 35–46.

Pugsley, L. I.

1939. Factors influencing the vitamin A and D potency of grayfish liver oil, *Squalus sucklii* (Girard). Journal of the Fisheries Research Board of Canada, vol. 4, No. 5, pp. 405–408.

Radcliffe, Lewis.

1916. The sharks and rays of Beaufort, North Carolina. Bulletin of the U.S. Bureau of Fisheries, vol. 34, Doc. No. 882, pp. 241–284, pls. 38–49.

Ribiero, Alipio de Miranda.

1923. Fauna Braziliense, Peixes, vol. 2.

Ripley, William Ellis.

1946. The soupfin shark and the fishery. California Division of Fish and Game, Fish Bulletin 64, pp. 6–37.

Ripley, William Ellis, and Rene A. Bolomey.

1946. The relation of the biology of the soupfin shark to the liver yield of vitamin A. California Division of Fish and Game, Fish Bulletin 64, pp. 39–72.

Rockwell, Robert H.

1916. Long Island sharks for the Museum. Brooklyn Museum Quarterly, vol. 3, No. 4, pp. 160–167.

Rosenblatt, Richard H., and Wayne J. Baldwin.

1958. A review of the eastern Pacific sharks of the genus *Carcharhinus*, with a redescription of *C. malapoensis* (Fowler) and California records of *C. remotus* (Dumeril). California Fish and Game, vol. 44, No. 2, pp. 137–159.

Schwartz, F. J.

1958. The cub shark, *Carcharhinus leucas*, taken at Flag Pond, Chesapeake Bay, Maryland. Maryland Tidewater News, vol. 14, No. 4, pp. 14 and 16.

Smith, Homer W.
1936. The retention and physiological role of urea in Elasmobranchii. Biological Reviews, vol. 11, pp. 49–81.

Springer, Stewart.
1938. Notes on the sharks of Florida. Proceedings of the Florida Academy of Science, vol. 3, pp. 9–41.
1940. The sex ratio and seasonal distribution of some Florida sharks. Copeia, No. 3, pp. 188–194.
1946. A collection of fishes from the stomachs of sharks taken off Salerno, Florida. Copeia, No. 3, pp. 174–175.
1949. An outline for a Trinidad shark fishery. Proceedings of the Gulf and Caribbean Fisheries Institute, 2d annual session, pp. 17–26.
1950. A revision of North American sharks allied to the genus *Carcharhinus*. American Museum Novitates, No. 1451, pp. 1–13.
1951. The effect of the availability of sharks on a shark fishery. Proceedings of the Gulf and Caribbean Fisheries Institute, 4th annual session, pp. 140–145.
1954. Laboratory experiments with shark repellents. Proceedings of the Gulf and Caribbean Fisheries Institute, 7th annual session, pp. 159–163.
1957. Some observations on the behavior of schools of fishes in the Gulf of Mexico and adjacent waters. Ecology, vol. 38, No. 1, pp. 166–171.

Springer, Stewart, and Price M. French.
1944. Vitamin A in shark liver oils. Industrial and Engineering Chemistry, vol. 36, p. 190.

Sprissler, G. Paul.
1942. An investigation of the proteinase of the gastric mucosa of shark. Catholic University of America, Contributions from Biological Laboratory, No. 42, pp. 1–52.

Strasburg, Donald W.
1958. Distribution, abundance, and habits of pelagic sharks in the Central Pacific Ocean. U.S. Fish and Wildlife Service, Fishery Bulletin 138, vol. 58, pp. 335–361.

Templeman, Wilfred.
1944. The life-history of the spiny dogfish (*Squalus acanthias*) and the vitamin A values of dogfish liver oil. Newfoundland Department of Natural Resources Research Bulletin No. 15 (Fisheries), pp. 1–102.

Thorne, Edwin.
1916. Occurrence of ground sharks, *Carcharhinus*, in Great South Bay. Copeia, No. 35, pp. 71–96.

Tortonese, Enrico.
1938. Revisione degli Squali del Museo Civico di Milano. Atti della Società Italiana di Scienze Naturali, vol. 77, pp. 283–318.
1951. Studi sui Plagiostomi V, Ulteriori considerazioni sulle specie Mediterranee dei generi *Sphyrna* e *Carcharhinus*. Doriana, Supplemento agli Annali del Museo Civico di Storia Naturale "G. Doria", vol. 1, No. 20, pp. 1–8.
1956. Fauna d'Italia, vol. 2, Leptocardia, Ciclostomata, Selachii. Edizioni Calderini, Bologna, pp. 1–332.

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GROWTH OF BLUEFIN TUNA OF THE WESTERN NORTH ATLANTIC

BY FRANK J. MATHER III AND HOWARD A. SCHUCK

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ABSTRACT

Growth of bluefin tuna *Thunnus thynnus* (Linnaeus) based on specimens captured mostly in the Cape Cod and Long Island areas was studied by counting annuli on scales and vertebrae and by analyzing length-frequency data. Similar results obtained by these two methods support their validity for ages 0–4. Older ages were determined by counting annuli only, but tag returns and weight-frequency data afford some corroboration for ages 5–7. Growth is believed to be extremely rapid during the first summer and about four-fifths of an inch per month in the first winter. During the next 3½ years, bluefin tuna grow at a rate of about 1¼ inches per month in summer and about one-third of an inch per month in winter, or about 7 inches per year. Tables of estimated sizes for each month of the first 5 years of life, and at midsummer through the age of 10 years, are presented. The growth rate appears to decline gradually to about 4 inches per year in this range. Only slight differences were found between the sizes and growth rates of fish of the same age taken in different years.

GROWTH OF BLUEFIN TUNA OF THE WESTERN NORTH ATLANTIC

By Frank J. Mather III and Howard A. Schuck

Information on the growth of bluefin tuna (*Thunnus thynnus*) of the western North Atlantic Ocean is incomplete, and limited to the smaller sizes for which age-with-length studies are published (Westman and Gilbert, 1941; Westman and Neville, 1942). Only fragmentary data are available on specimens longer than 46 inches. As a result of the growing interest in bluefin tuna by sport and commercial fishermen, we began a cooperative project, in 1950, to accumulate material for an age-determination study of the bluefin throughout its entire size range. The present paper is an account of our interpretation of this material to date.

In the preparation of this paper, we received valuable advice from Dr. Lionel A. Walford of the U.S. Bureau of Commercial Fisheries, and Dr. Henry B. Bigelow and Dr. William C. Schroeder, both of the Woods Hole Oceanographic Institution and Harvard University. Dr. James R. Westman of Rutgers University made available to us his extensive data on bluefin tuna. Other material was collected and measurements were obtained through the kindness of several Cape Cod commercial fishermen, notably Capts. John Vetorino, Adam Rupkus, Mike Goulart, and Nathaniel Wixon of Barnstable; also John A. Worthington of North Truro, Joseph Francis and Stuart Joseph of Provincetown, as well as through the cooperation of many sport fishermen and charter boat captains. Many of the length measurements were made by Frank Riley of the U.S. Bureau of Commercial Fisheries at Provincetown, Mass. Several other people contributed length measurements as noted in the frequency tables. Assistance in obtaining and processing data and in preparing this paper was received from members of the U.S. Bureau of Commercial Fisheries at Woods Hole, including Donald M. Allen who worked 4 years on this study, also from several members of the Woods Hole Oceanographic Institution. Their assistance is gratefully acknowledged.

READINGS OF ANNULI

As in other species of fishes, including several other tunas, annuli are formed on the scales, and also on the centra of the vertebrae (Sella, 1929; Aikawa and Kato, 1938; Westman and Gilbert, 1941; Westman and Neville, 1942; Partlo, 1955). Because these annuli are not consistently distinct in either of these two structures, and for other reasons which will be explained later in the text, we examined both. In the beginning we assumed that the annuli which we counted were formed once each year and therefore indicated the age in years. For verification of this assumption we depend on the internal evidence furnished by our material, including consistency of the age determinations with analysis of length-frequency data.

Most of our data are from fish caught in the vicinity of Cape Cod in pound nets or by hook and line. We took scales or vertebrae (or both) from as many specimens as time and opportunity permitted. There was rarely any difficulty in obtaining scales from fishermen's catches. This was less true for vertebrae, for frequently we were permitted to take them only from the tail, which is usually cut off in dressing the fish. Owing to unfavorable working conditions, it was not always possible to measure the fish from which the tails were cut. In such cases, we estimated the length from a regression of fork length against caudal spread [1] or, if the weight of the fish could be obtained, from a length-weight curve based on 778 specimens from 34 to 270 centimeters long.

We prepared celluloid impressions of the scales (Arnold, 1951), and studied them with the aid of a magnifying projector. Figure 1 shows the annuli, zones of crowding, or discontinuity of the circuli, which research workers consider to be formed annually. We also counted the rings on the centra of the vertebrae (fig. 2). These rings were marked

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[1] Regression formula with a correlation coefficient of 0.997 computed from 155 specimens, 29 to 270 centimeters long, where X is fork length, Y is caudal spread—Log X=0.7271+0.8642 Log Y.

Note.—Frank J. Mather III, Woods Hole Oceanographic Institution, Woods Hole, Mass.; Howard A. Schuck, Alaskan Air Command, Anchorage, Alaska, formerly fishery biologist, U.S. Bureau of Commercial Fisheries, Woods Hole, Mass.

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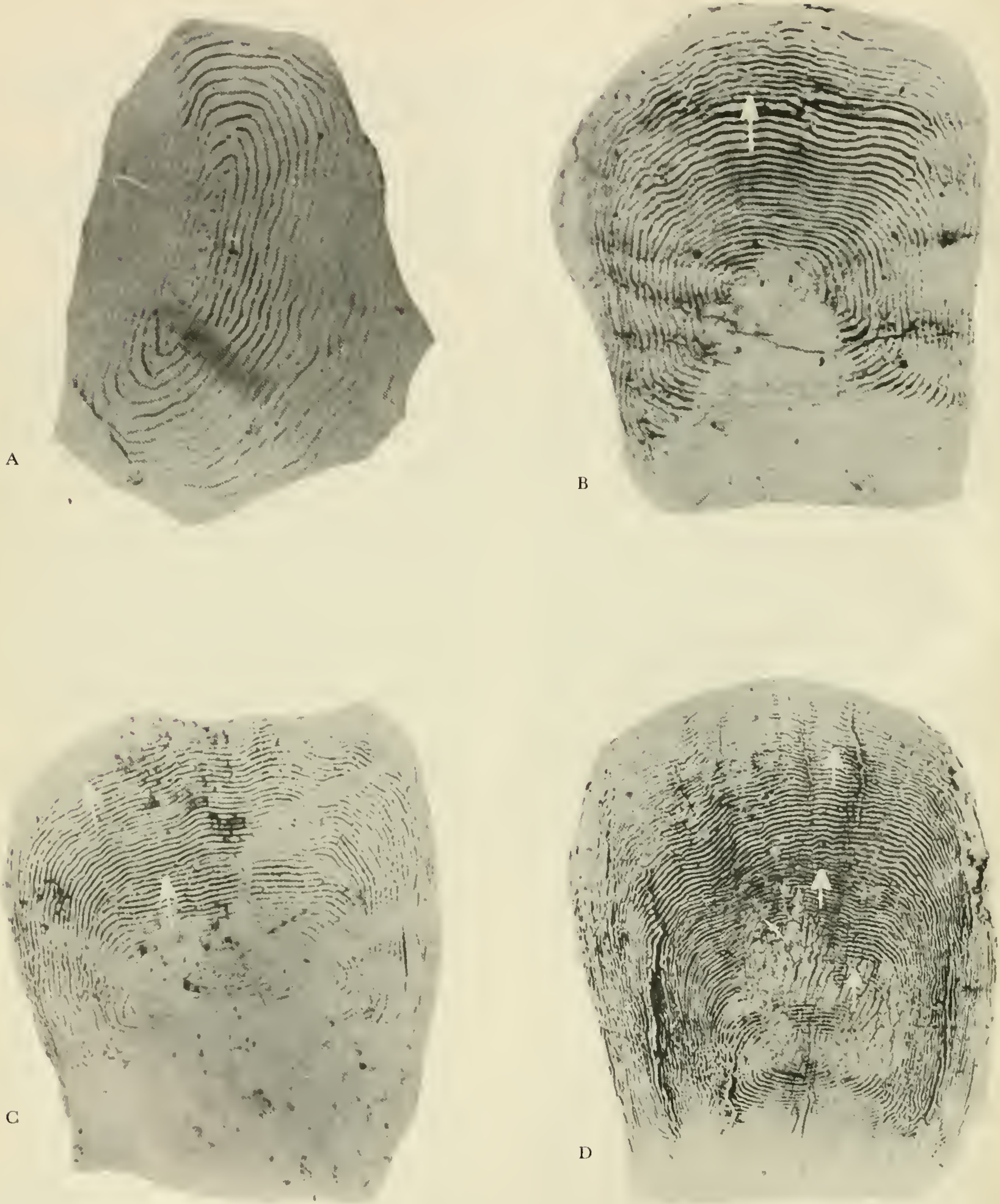

FIGURE 1.—Projected impressions of scales of bluefin tuna. Arrows indicate annuli. A. Scale from fish 34 cm. long taken off Martha's Vineyard, September 1952; no annulus. B. Scale from fish 60 cm. long taken off Martha's Vineyard, July 1950; 1 annulus. C. Scale from fish 80 cm. long taken off Martha's Vineyard, August 1952; 2 annuli. D. Scale from fish 104 cm. long taken off Cape Cod, October 1950; 3 annuli.

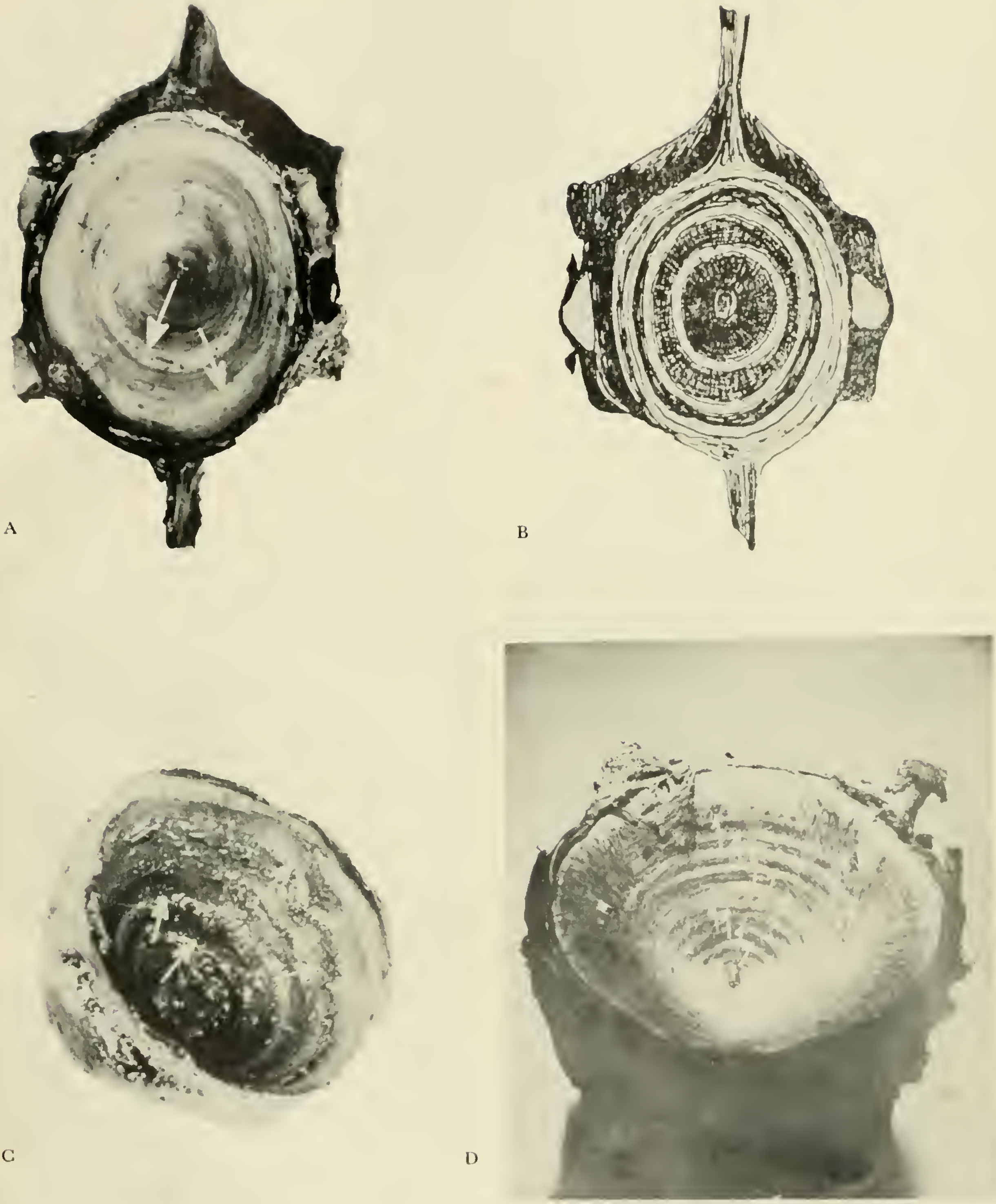

Figure 2.—Centra of vertebrae of bluefin tuna. Arrows indicate annuli. A. Vertebra from fish 77.5 cm. long taken off Martha's Vineyard, August 1951; 2 annuli. B. Drawing of stained vertebra from a fish 104 cm. long, taken off Cape Cod, October 1950; 3 annuli. Scale in figure 1D is from the same fish. (Reproduced from Galtsoff (1952) by permission of the author and publishers.) C. Stained vertebra of fish 110 centimeters long taken off Cape Cod, October 1950; 4 annuli. D. Vertebra of giant tuna taken off Cape Cod; about 11 annuli. Annuli beyond the 9th or 10th are usually small and indistinct and disappear soon after dissection. (A, C, and D, unretouched.)

TABLE 1.—*Fork lengths (in cm.) of bluefin tuna taken in the vicinity of Cape Cod, for each number of annuli*

[Numbers in parentheses estimated from regression of length on caudal spread or on weight]

0	1	2	3	4	5	6	7	8	9	10	11	12	13	14
34.2	51.5	71.0	84.0	107.2	(120.3)	(144.4)	155.8	162.9	179.0	182.0	223.4	207.5	236.6	247.0
35.3	52.1	71.0	84.7	107.7	(124.5)	(145.0)	156.7	170.8	179.4	184.5	225.6	229.0	237.0	248.0
(37.5)	52.2	73.0	85.3	108.0	(126.0)	(151.5)	(157.6)	174.8	183.0	190.4		234.0	240.0	(249.0)
37.8	53.3	74.0	85.7	108.6	126.2	153.0	(161.7)	176.5	185.2	218.0		241.5	240.6	
41.2	53.8	74.0	85.7	110.0	(127.1)	(153.2)	(164.4)	176.6	193.6	221.5		244.3	244.0	
42.2	55.4	74.0	85.9	110.0	(129.0)	(153.7)	(165.8)	177.8	(196.6)	224.0		245.7	248.0	
	56.0	74.5	85.9	112.1	130.0	154.0	(169.0)	182.0					257.0	
	56.1	74.7	86.1	(113.7)	(130.4)	(156.0)								
	58.2	74.8	87.1	114.1	130.8	158.2								
	58.8	74.9	87.4	114.5	(131.3)	(158.7)								
	59.0	75.0	87.8	114.6	132.0	(166.0)								
	59.7	75.0	88.2	115.0	(132.0)	(170.9)								
	60.0	75.6	88.4	115.0	(132.0)									
		75.7	88.7	116.1	(133.0)									
		75.7	89.0	116.6	(133.5)									
		76.3	89.0	117.5	(134.0)									
		76.7	89.7	(118.3)	135.0									
		76.9	90.2	118.5	135.0									
		77.1	90.8	(118.6)	(135.5)									
		77.5	91.1	(119.0)	(137.2)									
		77.5	91.6	119.6	(137.4)									
		77.6	92.1	120.0	140.0									
		(77.9)	92.9	122.0	140.0									
		78.2	95.0	(122.8)	(140.0)									
		78.5	(98.0)	(123.0)	142.2									
		79.1	103.3	124.4	146.0									
		79.5	104.4	124.5	(150.2)									
		80.0	104.8	125.6	(157.0)									
		(80.8)		129.0	(160.3)									
		(81.8)		(130.2)										
		81.9		(130.4)										
				(130.7)										
				(132.1)										

by depressions in the surface and also by variations in color, which were accentuated when the vertebrae were soaked in water, or when they were stained (Galtsoff, 1952). We examined the vertebrae either with the naked eye or with the aid of a wide-field binocular microscope. We believe that these annuli on scales and vertebrae are probably formed during winter or early spring.

Scales were legible for most fish weighing 50 pounds or less, but rarely for larger ones. As scales could be more readily collected than vertebrae, we used scales for most of our age determinations of small fish, resorting to vertebrae for larger specimens. The material from each specimen was usually examined independently, and often also by our colleague Donald Allen. When readings differed, material was reexamined. If the difference between extremes remained greater than 2, the specimen was discarded. For differences of 2 or less, the average value or the unit closest to it was used. Actually, there were few disagreements in readings for fish up to 50 or 60 pounds. Legible scales and vertebrae were found for 28 fish and counts of annuli on scales agreed with those on the vertebrae. Readings for fish of 70 to 270 pounds often differed by 1 year; those for larger fish sometimes differed by 2 years or more. Lengths (table 1) are from annuli counted from scales or vertebrae, or both; length-frequency distributions (fig. 3) are for each year of age; average length (table 2) is for each year.

TABLE 2.—*Average fork length of bluefin tuna taken in the vicinity of Cape Cod, for each year of age from readings of annuli on scales and vertebrae*

Age in years	Length in cm.	Number of specimens
0	38.0	6
1	55.9	13
2	76.5	31
3	90.5	28
4	118.8	34
5	135.0	29
6	155.4	12
7	161.6	7
8	174.4	7
9	186.1	6
10	203.4	6
11	224.5	2
12	233.7	6
13	243.3	7
14	248.0	3

ANALYSIS OF LENGTH FREQUENCIES

Another method of estimating age and growth is by following the seasonal progression of dominant size groups. This is especially useful for species that spawn over a fairly short season and grow rapidly. Evidently the bluefin tuna meets these conditions, as even casual observers notice the regularity with which catches of small tuna can be ranked in size categories by eye. Moore (1952) and Postel (1954) analyzed size frequencies to determine the ages of yellowfin tuna in the Pacific and the tropical eastern Atlantic, respectively. Aikawa and Kato (1938) used the same method in conjunction with counts of vertebral rings in studying the growth of western Pacific tunas, as did Partlo (1955) for northeastern Pacific albacore. Westman and Gilbert (1941) and Westman and Neville (1942) used the method in conjunction with scale studies for bluefin tuna taken off Long Island, N.Y.

We have based our size-frequency study on lengths rather than on weights, as we believe that, for fish of a given age, lengths are subject to smaller and more regular variations. Because we lack sufficient data on the large sizes, we have not attempted to analyze lengths greater than 56.5 inches.

Table 3.—*Length frequencies of bluefin tuna from 20.5 to 56.5 inches long taken off Long Island*[1] *in 1941 and off New England*[2] *in 1950–57 from late June to mid-October*

Length in inches	Number of tuna							Age in years
	July		August		September		October	
	[3] 1–15	16–31	1–16	17–31	1–15	16–30	1–18	
21	7							I
22	9	31	4	1				
23	5	33	13	9	4	1		
24		25	17	31	42	4		
25		4	12	10	58	7	2	
26		1	1	1	26	14		
27	1	2		1		3		
28		5	3		1	2		
29	23	24	10	3				II
30	60	68	88	5	3	1		
31	57	114	122	41	1	1	2	
32	25	64	65	97	3	7	3	
33	10	28	22	72	3	15	8	
34	9	1	6	17	9	15	15	
35				4	6	5	9	
35	30	27	7	3				
36	69	50	44	13	4	5	4	
37	87	120	119	46	8	6	6	III
38	53	100	178	153	24	6	8	
39	14	56	141	253	40	26	22	
40	1	20	96	203	94	29	26	
41		7	31	112	76	28	18	
41	1	8						
42		2	9	33	52	23	10	
42	13	10	4					
43	19	15	11	11	16	14	5	
44					4	2	3	
44	28	17	18	23	8			IV
45	37	14	11	57	9	4	6	
46	58	11	8	23	8	2	11	
47	29	8	7	6	15	6	13	
48	24	3	4		9	4	21	
49	5	3	6		5	1	9	
49		1						
50	5	1		4	1		7	
51	5	2	2	1			7	
52	2			2		2	2	
53	5	2				2	1	
54	1	3				1	6	
55	2	2		4		2	6	
56	3			5	1	3	1	

[1] Westman and Neville's (1942) sample consisting of 1,129 fish, was measured at Freeport, L.I., (N.Y.).

[2] A few fish caught off Nova Scotia, Long Island (N.Y.), and New Jersey are included. Most of this sample was taken in the vicinity of Cape Cod, but many of the fish were from the offshore waters, mostly in the vicinity of Georges Bank. Frank Riley measured 1,891 fish at Provincetown (Mass.) in 1953–54. We are indebted to Lewis R. Day of the Fisheries Board of Canada for measuring 5 fish in Nova Scotia in 1950, Jean McClean Wight of West Hartford (Conn.) for measuring 5 fish in Nova Scotia in 1954, Capt. Charles A. Mayo, Jr., of Provincetown (Mass.) for measuring 57 fish there in 1956, and Dr. Robert H. Gibbs, Jr., recently of the Woods Hole Oceanographic Institution, for measuring 69 fish in the Cape Cod area in 1956 and 1957. The remainder of the sample was measured by the authors and Donald M. Allen.

[3] Includes 102 fish measured June 28–30, 1953.

From various sources, we have compiled length measurements of 4,990 bluefin tuna less than 56.5 inches long. With the exception of the 1941 sample which was measured on Long Island by Westman and Neville (1942), and several fish less than 20 inches long which were from more southerly waters, most of these were taken in the New England area from 1950 to 1957. With the exception of a few specimens less than 20 inches long, the fish were caught from late June to mid-October. We have followed the method of Westman and Neville in measuring the fish to the nearest inch with a tape from the snout to the fork of the tail, following the curvature of the body. Where we used calipers for determining length, we estimated the "curved" measurement from a conversion factor.[2] The measurements for fish more than 20 inches long, for all localities and years combined, are listed by half monthly periods in table 3. The data for smaller fish were gathered from more diverse localities and extend over a greater portion of the year, hence are listed in more detail in table 4.

Table 4.—*Lengths of bluefin tuna less than 20 inches long, with dates and localities of capture and sources*

Date	Length in inches	Number of fish	Locality	Source
June 9, 1953	1.8	1	Miami area, Fla.	Rivas (1954).
July 14, 1953	11.7	1	do	Do.
July 17, 1953	12.3	1	do	Do.
July 19, 1953	10.3	1	do	Do.
July 16–23, 1954	12.0	1	Atlantic City, N.J.	William Upperman.[1]
July 19–26, 1954	9.0	1	do	Do.
July 23, 1953	11.4	1	Miami area, Fla.	Rivas (1954).
July 23, 1957	7.7	1	do	Al Pflueger.[2]
July 24, 1953	11.8	1	do	Rivas (1954).
Do	12.9	1	do	Do.
July 25, 1954	12.7	1	do	Al Pflueger.[1]
July 26, 1953	11.9	1	do	Rivas (1954).
July 29, 1953	12.2	3	do	Do.
Do	13.5	1	do	Do.
July 30, 1953	11.2	1	do	Do.
July 31, 1953	11.7	1	do	Do.
July 31, 1954	12.0	2	do	Al Pflueger.[2]
Aug. 10, 1953	12.4	1	do	Rivas (1954).
Aug. 12, 1954	13.0	1	Brielle, N.J	Mrs. K. R. Mayer.[3]
Aug. 23, 1940	14.2	1	do	Manasquan Marlin and Tuna Club.
Aug. 25, 1953	9.0	1	do	Mrs. K. R. Mayer.[3]
Aug. 29, 1938	12.7	1	do	C. W. Hoffman.[1]
Aug. 29, 1952	15.5	1	Off Martha's Vineyard, Mass.	R/V *Bear*, R. Wolf.[2]
Sept. 2, 1939	12.5	1	Brielle, N.J	Westman and Gilbert (1941).
Sept. 1–7, 1953	12.7	4	Gulf of Mexico, (29°03′ N, 88°54′ W).	U.S. National Museum.[4]
Do	13.8	1	do	Do.[4]

See footnotes at end of table.

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[2] A straight line fitted by inspection to a plot of straight (caliper) length against curved (tape) length, based on measurements for 185 individuals 37 to 257 cm. long, indicated that straight length was 0.958 of curved length.

TABLE 4.—*Lengths of bluefin tuna less than 20 inches long, with dates and localities of capture and sources*—Continued

Date	Length in inches	Number of fish	Locality	Source
Sept. 5, 1953	16.0	2	Brielle, N.J	Mrs. K. R. Mayer.[3]
Do	16.5	1	do	Do.[3]
Sept. 5, 1957	12.0	1	Ocean City, Md	F. J. Mather.
Sept. 6, 1952	15.6	1	Off Martha's Vineyard, Mass.	Do.
Sept. 7, 1957	12.0	1	Ocean City, Md	M. L. Dennis.
Do	13.0	1	do	Do.
Sept. 12, 1952	15.0	1	Off Long Island, N.Y.	Rivas (1954).
Sept. 12, 1953	9.8	1	Brielle, N.J	Mrs. K. R. Mayer.[3]
Do	11.0	1	do	Do.[3]
Do	14.0	- 3	do	Do.[3]
Sept. 14, 1957	13.2	20	Ocean City, Md	M. L. Dennis.
Sept. 15, 1953	18.0	1	Brielle, N.J	Mrs. K. R. Mayer.[3]
Sept. 17, 1952	14.1	1	Off Martha's Vineyard, Mass.	R/V *Caryn*, F. J. Mather.
Sept. 18, 1952	16.9	1	do	Do.
Sept. 20, 1957	14.0	1	Ocean City, Md	M. L. Dennis.
Sept. 21, 1954	13.9	1	Off the Carolinas, (33°10′ N, 77°25′ W).	U.S. Fish and Wildlife, Brunswick, Ga.
Sept. 21, 1957	31.0	3	Ocean City, Md	M. L. Dennis.
Do	14.0	1	do	Do.
Sept. 22, 1957	14.0	1	do	Do.
Do	15.0	1	do	Do.
Sept. 23–24, 1953	17.4	1	Off Martha's Vineyard, Mass.	M/V *Albatross III*, J. Taylor.[2]
Sept. 24, 1957	13.0	1	Ocean City, Md	M. L. Dennis.
Do	14.0	10	do	Do.
Do	15.0	6	do	Do.
Oct. 11, 1953	15.0	1	Brielle, N.J	Mrs. K. R. Mayer.[3]
Oct. 13, 1952	14.5	1	Cape Hatteras, N.C.	F. J. Mather.
Oct. 18, 1953	17.0	4	Brielle, N.J	Mrs. K. R. Mayer.[3]
Nov. 10, 1953	15.6	1	Miami area, Fla	Rivas (1954).
Nov. 12, 1952	17.7	1	do	Do.
Nov. 16, 1952	16.6	1	do	Do.
Nov. 27, 1952	17.6	1	do	Do.
Jan. 5, 1951	18.3	1	do	Do.
Jan. 27, 1959	18.8	3	Off Cape Hatteras, N.C.	M/V *Albatross III*. R. Brigham and L. Lawday.[2]

[1] Measurements were checked with ruler on photographic prints.

[2] Specimens were made available to us by kindness of the individuals listed.

[3] Measurements taken by charter boat captains who tagged the tuna, and collected for us by Mrs. Mayer.

[4] Measurements were made by Isaac Ginsburg and transmitted to us by Dr. L. P. Schultz.

The length frequencies for all localities combined between late June and mid-October are shown graphically for each half monthly period by years in figures 4–10, and for all years combined, by half monthly periods in figure 11. The number of fish in any given size group and period varies considerably from year to year, due to nonuniform sampling and availability, and to variations in the numerical strength of year classes. The general pattern of size groupings is consistent, however, with maximum and minimum numbers occurring around the same lengths year after year. It seems obvious that these groupings represent different ages. We have arbitrarily designated with vertical lines the points which we believe best separate the various age groups. Usually there seems to be little question as to where these lines should be drawn. If doubtful we based our judgment on a comparative study of data for the entire series of years. In a few such cases, we assigned some of the fish at a low point to one age and the rest to the other. Corresponding broken lines separate the data in table 3.

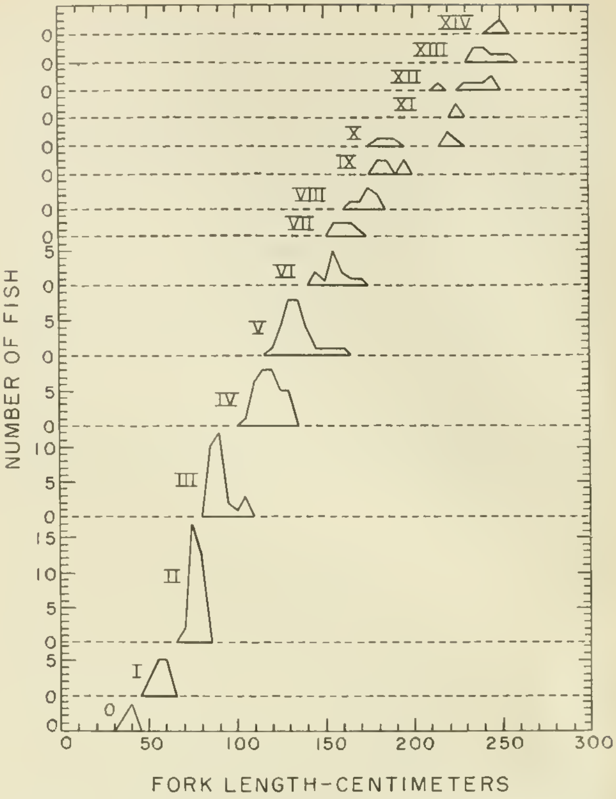

FIGURE 3.—Frequency distribution by 5-centimeter groups of lengths of bluefin tuna for counts of annuli.

AGE DETERMINATION

The question arises as to whether or not the fish forming the first modal group appearing in our length frequency study are young of the year. In figure 12, we have compared the lengths of fish in each age group as determined by counts of annuli with the lengths of those in corresponding age groups as determined by length frequencies. On examining this figure, we find the assumption that fish in the first modal group are young of the

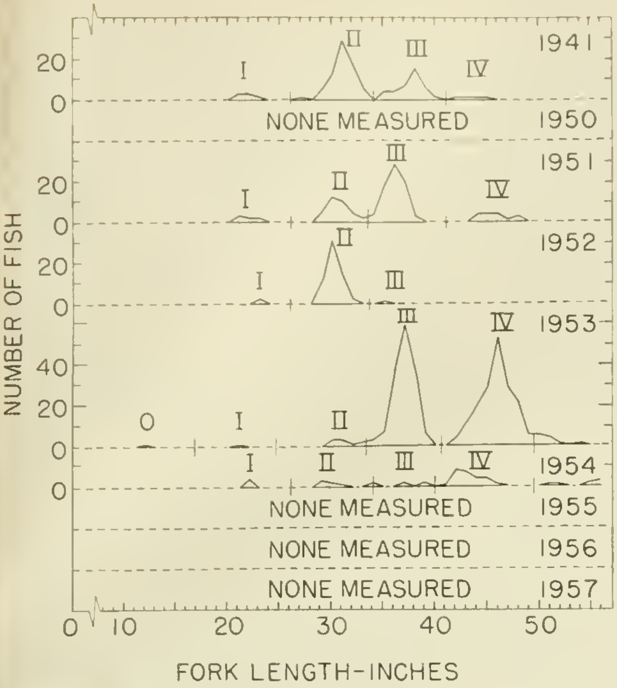

FIGURE 4.—Frequency distribution by 1-inch groups of lengths of bluefin tuna taken July 1–15, by years. The 1953 sample includes 102 fish measured June 28–30.

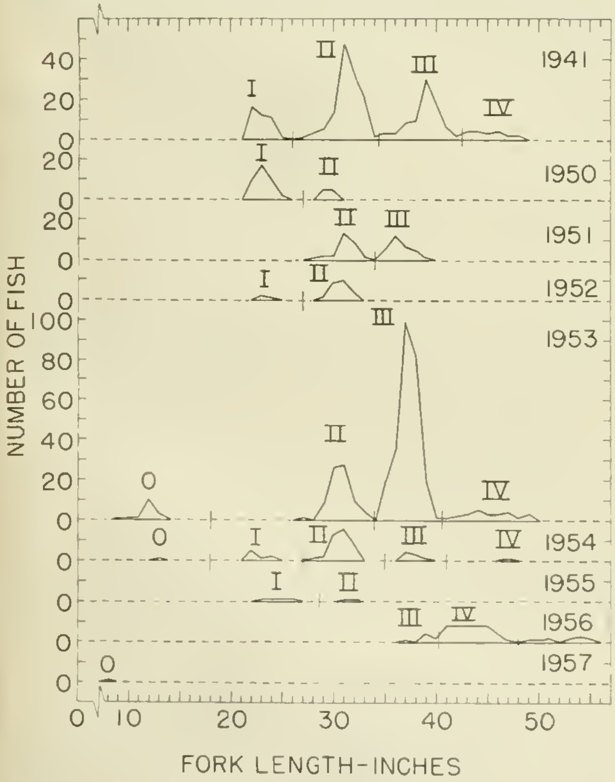

FIGURE 5.—Frequency distribution by 1-inch groups of lengths of bluefin tuna taken July 16–31, by years.

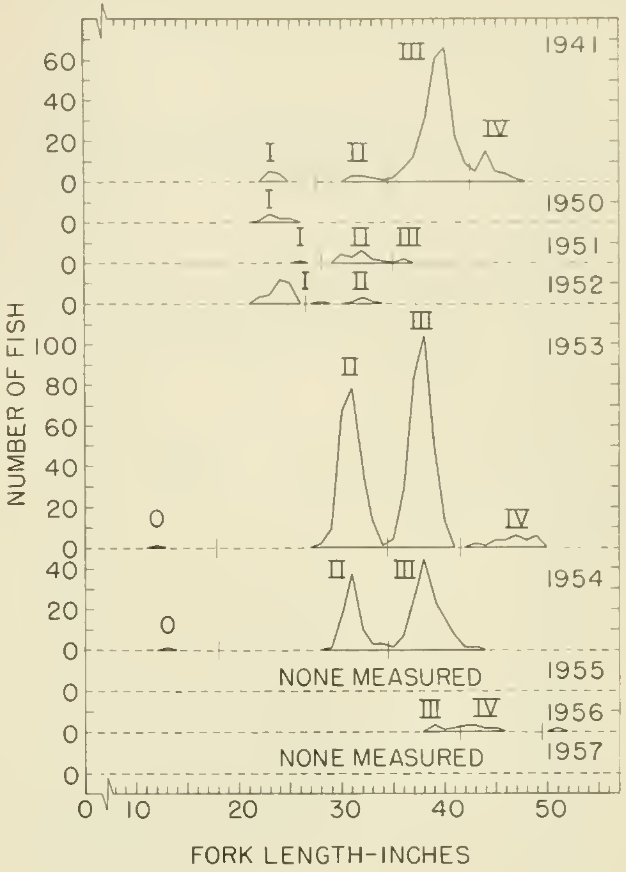

FIGURE 6.—Frequency distribution by 1-inch groups of lengths of bluefin tuna taken August 1–16, by years.

year is supported by the fact that no annuli are found on scales and vertebrae of fish of this size. Moreover, it is in accord with the conclusions of Sella (1929) and others studying the European bluefin tuna, which were officially accepted by the International Council for Exploration of the Sea in 1932 at Malaga (Conseil International pour l'Exploration de la Mer, 1933), and with those reached by Westman and Gilbert (1941), Westman and Neville (1942), and by Rivas (1954), for bluefin taken off New York and Miami, Fla. It is supported by our failure in all our observations, inquiries, and searching of literature and records, to find any evidence that a smaller size group exists. We conclude therefor that tuna in the second size group (corresponding to fish with 1 annulus) are 1 year old; in the third size group (2 annuli) are 2 years old; and so on through 4

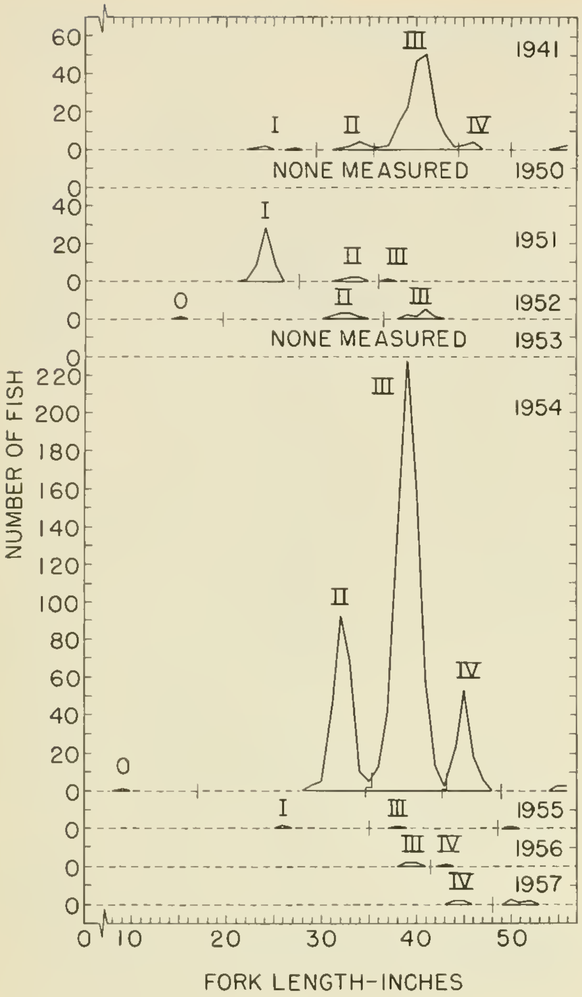

FIGURE 7.—Frequency distribution by 1-inch groups of lengths of bluefin tuna taken August 17–31, by years.

years. Although length data on older ages are not sufficient for analysis, we believe that counts of annuli are useful for estimating the age of older fish despite the decreasing reliability of readings with increasing age.

We find also that the analysis of length-frequency curves is consistent with age determinations by counts of annuli on scales and vertebrae. Such discrepancies as exist probably result from the fact that the samples for age readings were smaller and less uniformly distributed through the seasons than were those taken for length measurements. For example, most of our samples for counts of annuli of 3-year-olds were collected in early summer or fall rather than in midsummer. Even so, correspondence in conclusions reached from the two kinds of data is close.

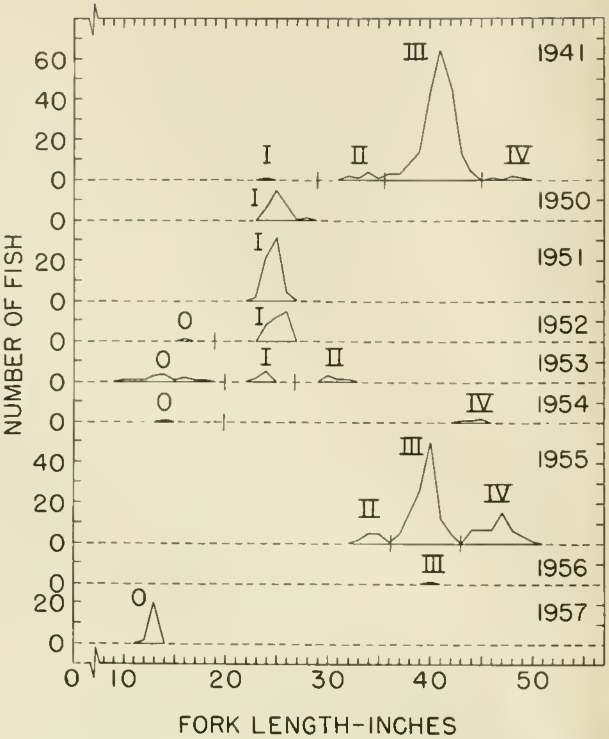

FIGURE 8.—Frequency distribution by 1-inch groups of lengths of bluefin tuna taken September 1–15, by years.

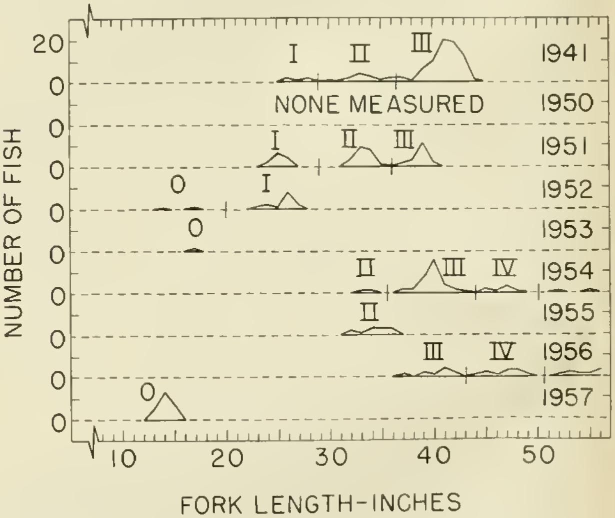

FIGURE 9.—Frequency distribution by 1-inch groups of lengths of bluefin tuna taken September 16-30, by years.

Weight frequencies of landings of medium-sized bluefin tuna in Cape Cod Bay and Nova Scotia in the years 1948–51 (fig. 13) show a tendency for modal weights to coincide with sizes determined by counts of annuli for ages 5–7. Most clear cut cases are the 5-year-olds in Cape Cod Bay and 6-year-olds in Nova Scotia in 1948,

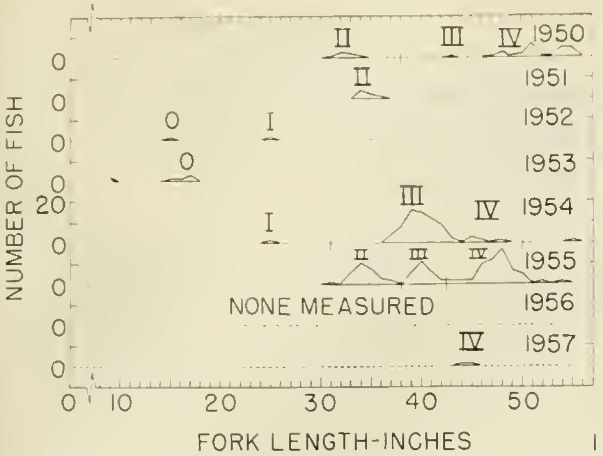

Figure 10.—Frequency distribution by 1-inch groups of lengths of bluefin tuna taken October 1–18, by years.

and the 6-year-olds in Nova Scotia in 1949. Split modes show a preponderance of 7-year-olds in both areas in 1950, suggesting the progression of the year class of 1943 through the Cape Cod Bay fishery 1948–50 and the Nova Scotia fishery 1949–50.

Two successful tagging experiments with bluefin tuna yielded approximate data on their actual growth. One fish, tagged off Cape Cod, Mass., July 27, 1954, was recaptured by French fishermen in the Bay of Biscay August 16, 1959. When tagged, the fish measured 72.5 cm., and its weight when recaptured was reported as approximately 65–70 kilograms (143–154 pounds equivalent to about 150–154 cm.). These sizes are near the lower limits for ages 2 and 7, respectively, from table 1. The other was tagged August 11, 1957, off Chatham, Mass., and recaptured August 30, 1959, off Gloucester, Mass. Its weight when tagged was estimated as 65 pounds (equivalent to about 114 cm.) by an experienced fisherman, and it weighed 130 pounds (equivalent to about 150 cm.) when recaptured. These lengths are in good agreement with those listed in table 1 for ages 4 and 6, respectively. Hence the results of these experiments are in reasonable agreement with our age determinations by counts of annuli.

GROWTH OF YOUNG BLUEFIN TUNA

As length measurements are several times as numerous as counts of annuli, and permit us to trace growth during each summer as well as from year to year, we shall base our discussion of growth of young tuna on length frequency analysis.

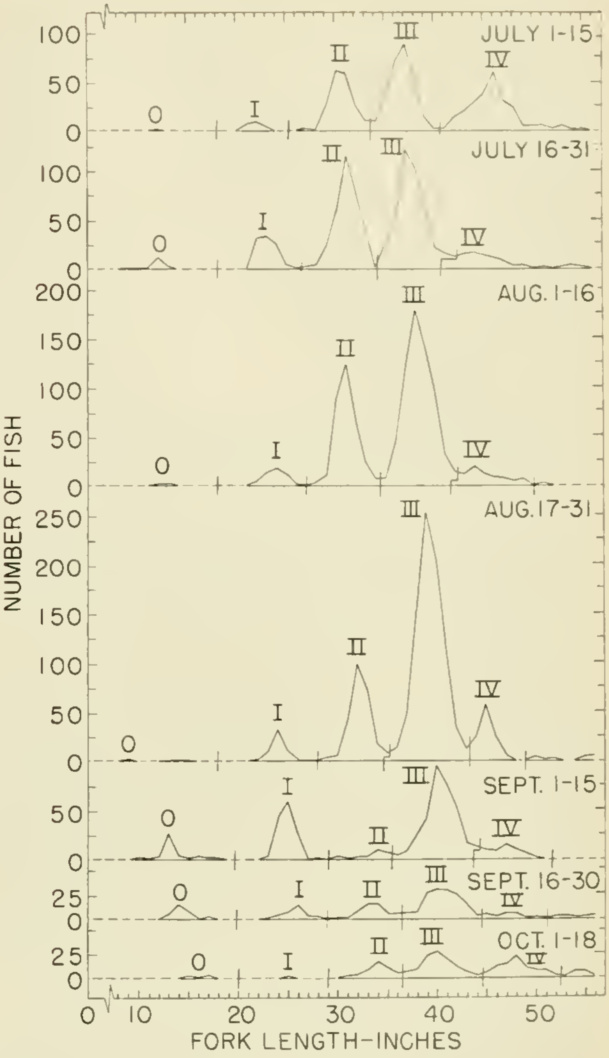

Figure 11.—Frequency distribution by 1-inch groups of lengths of bluefin tuna taken in 1941 off Long Island and in 1950–57, mostly off New England, by periods. Three very small tuna taken off New Jersey in 1938–40 are also included.

Table 5 lists the average lengths of the fish in each age group of fish more than 20 inches long, as demarcated by vertical lines in figures 4–11. It identifies year classes and also shows average lengths for all years combined. We plotted these lengths by periods in figure 14 and fitted curves to them empirically, taking into account the number of measurements represented by each point, except in 2 or 3 where the preponderant samples were not, in our opinion, composed of average-sized fish.

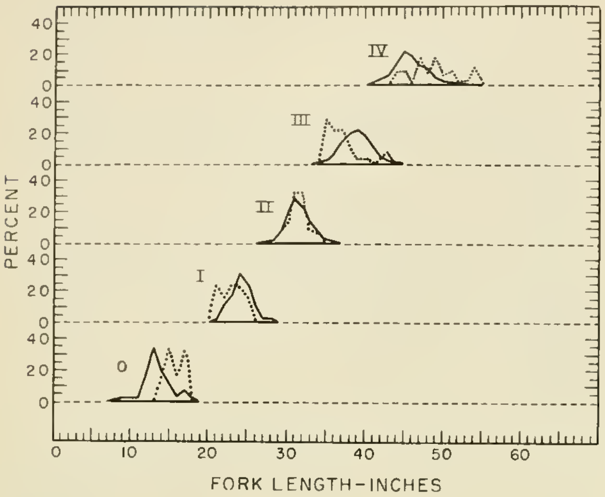

FIGURE 12.—Frequency distribution by 1-inch groups of lengths of bluefin tuna for age groups 0–IV as determined by length frequencies (solid lines) and by counts of annuli (dotted lines).

The fish less than 20 inches long listed in table 4 obviously form a distinct age group. Figure 15 shows the averages of these measurements with a curve drawn by inspection to fit the points and also to fit in with the curve for 1-year-olds from figure 14. Although our unpublished studies of the distribution of the bluefin tuna indicate that all these fish belong to one population, samples from different areas have been designated by different symbols. Figure 16 shows a curve of estimated growth of bluefin tuna for the first 4½ years of life, and table 6 lists the average sizes at the middle of each month, as indicated by this curve.

Figure 16 indicates extremely rapid initial growth and distinct seasonal variations in growth rate. Bluefin tuna spawn during an undefined period in spring (Rivas, 1954; Bullis and Mather, 1956). Assuming, as we did in drawing figure 16, that hatching occurs in mid-May, the young may grow at a rate of nearly 6 inches per month to reach a size of 8½ inches by July 1. In the ensuing discussion, however, we shall consider July 1 as the date of birth and shall refer to the period July 1–October 16 as "summer" and the remainder of the year as "winter." The growth rate diminishes rapidly during the first summer, but the average rate is estimated at 2 inches per month. The rate continues to decrease during most of the first winter, averaging about four-fifths of an inch per month. For the remainder of the period studied, ages 1–4, the growth rate does not change greatly with age, averaging about 1½ inches per month in summer and about one-third of an inch per month in winter.

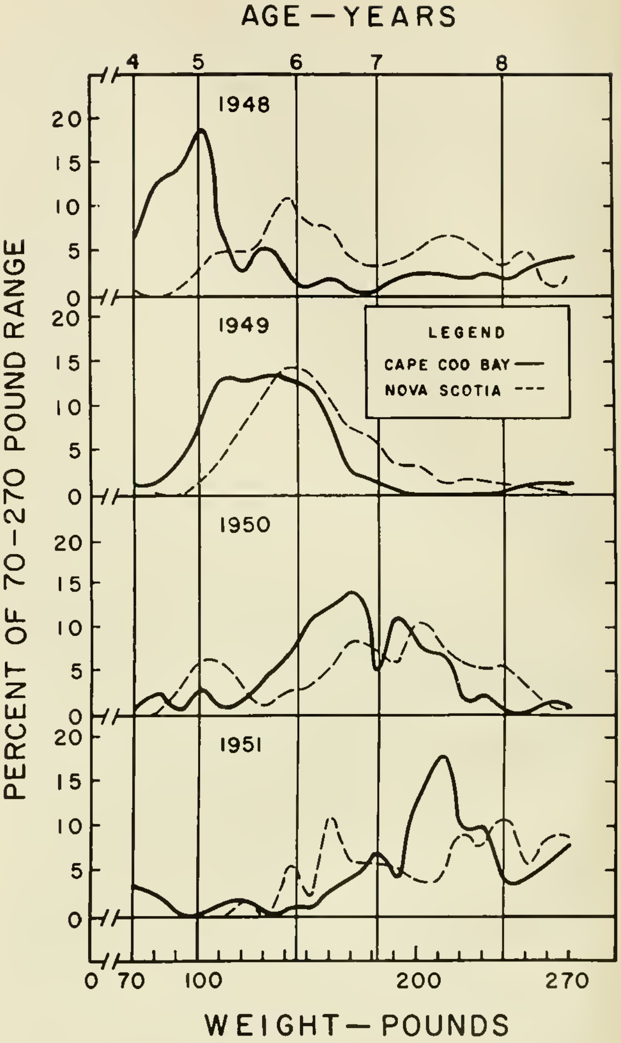

FIGURE 13.—Weight frequencies by 10-pound groups of bluefin tuna from 70 to 270 pounds, taken in Cape Cod Bay and off Nova Scotia in 1948–51, by years.

ESTIMATED ANNUAL GROWTH OF BLUEFIN TUNA THROUGH 10 YEARS

The average sizes at each age, determined by length frequency analysis for ages 0–4, and by counts of annuli for older ages, are plotted in figure 17. The curve shown was derived graphically, starting from the point for 3-year-olds, from the

Walford (1946) transformation of our data. As we found it possible to read only a small percentage of the material available for ages beyond 10 years, we have drawn the curve to that point only. Average sizes at mid-summer for bluefin tuna of ages 0–10 as indicated by this curve are listed in table 7.

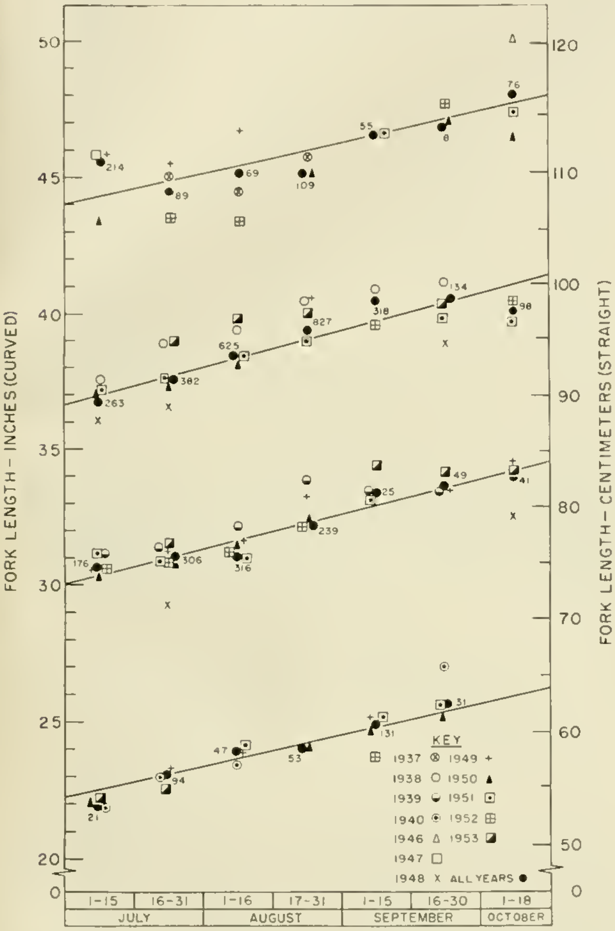

Figure 14.—Average lengths of bluefin tuna by age groups as indicated in figures 4 to 11. Curves were fitted empirically. The numbers of fish in the samples for all years combined are indicated. Samples consisting of less than 5 fish were not shown.

CONCLUSIONS

Our results through the fifth summer of life for bluefin tuna taken off New England are substantially in agreement with those of Westman and Neville (1942) for fish taken off Long Island. Our study of the growth of these young tunas, however, was based on a much larger sample, and the sampling was spread over several years rather than 1 year. Differences in growth between year classes were found to be slight and the results of the analysis of the composite sample are believed to approximate the average encountered in nature. Although it was not possible to fully verify the readings of annuli for older fish by the analysis of size frequencies, and difficulties in reading the annuli increased with their number, we have extended our determinations to considerably older ages than has previously been done for western Atlantic bluefin tuna.

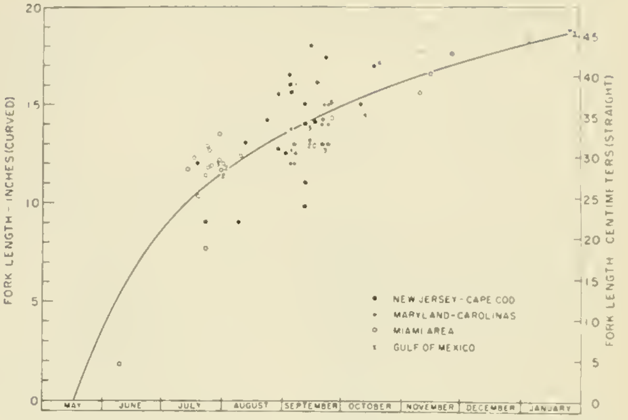

Figure 15.—Lengths of bluefin tuna less than 20 inches long (young of the year), from table 4. The curve of estimated growth was fitted by inspection.

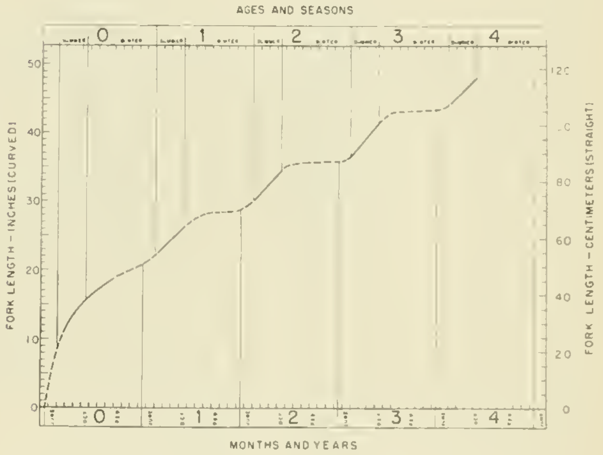

Figure 16.—Estimated growth of young bluefin tuna. Broken lines indicate estimated lengths in periods for which data are lacking. The upper scale shows ages and seasons as assumed in the text, and the lower scale shows ages assuming that hatching occurs at mid-May.

TABLE 5.—*Average lengths of bluefin tuna, in each age group as indicated in figures 4 to 11, listed by ages, years of measurement, and year classes*

Age in years	Year of measurement	Average lengths of fish in inches (numbers of fish in parentheses)							Year class
		July		August		September		October	
		1–15	16–31	1–16	17–31	1–15	16–30	1–18	
I	1941	21.8(7)	22.9(40)	23.4(9)	24.5(4)	24.0(1)	27.0(5)		1940.
	1950		23.1(39)	23.6(9)		25.2(29)			1949.
	1951	21.9(7)		26.0(1)	24.0(48)	24.6(59)	25.1(12)		1950.
	1952	23.0(2)	23.3(3)	24.0(28)		25.2(35)	25.6(14)	25.0(1)	1951.
	1953	21.0(1)				23.7(7)			1952.
	1954	22.0(4)	22.6(8)					25.0(1)	1953.
	1955		24.5(4)		26.0(1)				1954.
	All years	21.9(21)	23.1(94)	23.9(47)	24.1(53)	24.8(131)	25.6(31)	25.0(2)	All years.
II	1941	31.1(71)	31.3(126)	32.1(9)	33.8(9)	33.5(8)	33.3(14)		1939.
	1950		29.2(10)					32.5(7)	1948.
	1951	30.5(33)	31.2(29)	31.6(16)	33.2(5)		33.4(21)	34.6(7)	1949.
	1952	30.2(57)	30.7(25)	31.4(6)	32.3(9)				1950.
	1953	31.2(9)	30.7(75)	30.9(214)		31.1(5)			1951.
	1954	30.8(7)	30.6(39)	31.2(71)	32.2(216)		33.5(2)		1952.
	1955		31.5(2)			34.4(13)	34.2(12)	34.2(29)	1953.
	All years	30.6(176)	30.9(306)	31.0(316)	32.2(239)	33.3(25)	33.6(49)	33.9(41)	All years.
III	1941	37.5(37)	38.9(78)	39.3(208)	40.4(163)	40.8(202)	41.1(72)		1938.
	1950							43.0(1)	1947.
	1951	36.0(72)	36.5(30)	36.0(2)	37.0(1)		38.8(17)		1948.
	1952	35.0(1)			40.5(9)				1949.
	1953	36.9(147)	37.2(259)	37.8(285)					1950.
	1954	37.2(5)	37.6(8)	38.4(126)	39.0(648)		39.8(34)	39.8(65)	1951.
	1955				38.0(1)	39.6(113)		40.4(27)	1952.
	1956		39.0(7)	39.8(6)	40.0(5)	40.0(1)	40.3(10)		1953.
	All years	36.7(263)	37.5(382)	38.4(625)	39.3(827)	40.4(318)	40.5(134)	40.1(98)	All years.
IV	1941	43.5(4)	45.0(19)	44.4(30)	45.7(6)	47.9(4)			1937.
	1950							50.0(15)	1946.
	1951	45.8(16)							1947.
	1953	45.8(169)	45.5(24)	46.7(27)				48.0(1)	1949.
	1954	43.3(25)	47.0(1)		45.1(99)	44.3(4)	47.0(8)	46.3(6)	1950.
	1955					46.6(48)		47.4(55)	1951.
	1956		43.5(45)	43.4(10)			47.7(11)		1952.
	1957				44.5(4)			44.5(2)	1953.
	All years	45.5(214)	44.4(89)	45.1(69)	45.1(109)	46.5(55)	46.8(18)	48.0(76)	All years.

TABLE 6.—*Estimated sizes of young bluefin tuna at the middle of each month derived from figure 16*

Month	Fork length in inches curved measurement					Fork length in centimeters straight measurement					Weight in pounds				
	Age in years					Age in years					Age in years				
	0	I	II	III	IV	0	I	II	III	IV	0	I	II	III	IV
May	0	21.0	28.7	35.8	43.5	0	51.1	69.9	87.1	106.0	0	6.2	15.5	31.2	51.0
June	6.5	21.7	29.5	36.2	43.7	15.8	52.8	71.8	88.1	106.7	0.2	6.8	17.0	32.0	52.0
July	10.3	22.7	30.6	37.3	44.5	25.1	55.3	74.5	90.9	108.5	0.6	7.8	19.0	34.0	55.0
August	12.6	23.9	32.0	38.6	45.7	30.6	58.2	77.6	94.0	111.3	1.1	9.4	22.0	36.5	60.5
September	14.3	25.0	33.2	40.0	46.9	34.8	60.9	80.9	97.4	114.1	1.9	10.0	24.4	42.0	65.0
October	15.3	26.1	34.5	41.4	48.0	37.2	63.5	84.0	100.8	117.0	2.1	11.5	26.5	46.0	68.0
November	16.7	27.2	35.3	42.6		40.6	66.2	85.9	103.9		2.9	13.5	29.0	49.0	
December	17.6	27.8	35.4	43.0		42.9	67.7	86.2	104.8		3.5	14.2	30.0	49.5	
January	18.4	28.2	35.5	43.1		44.8	68.6	86.4	105.0		4.1	14.6	30.4	50.0	
February	19.1	28.3	35.6	43.2		46.5	68.9	86.6	105.1		4.6	14.9	30.6	50.2	
March	19.7	28.4	35.7	43.3		48.0	69.1	86.9	105.3		5.0	15.1	30.8	50.4	
April	20.2	28.5	35.8	43.4		49.1	69.4	87.1	105.7		5.4	15.3	31.0	50.7	

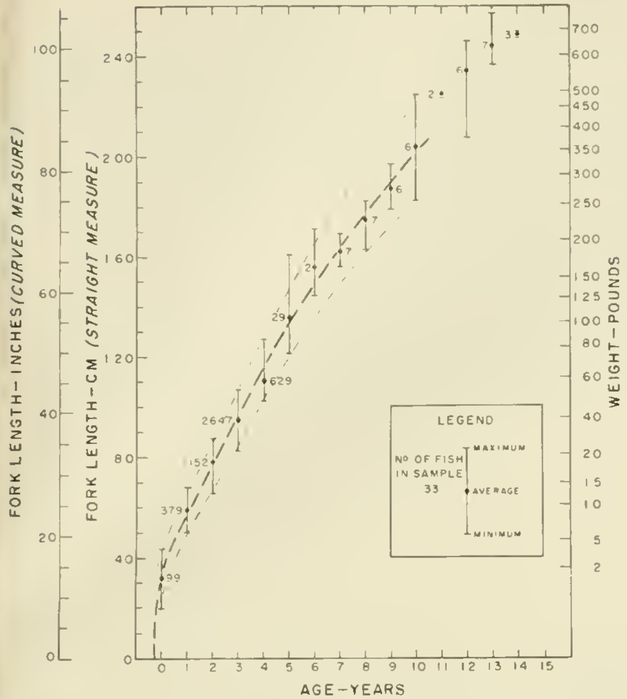

FIGURE 17.—Estimated growth curve for bluefin tuna (heavy broken line), with points derived from length frequencies for ages 0–IV years and from counts of annuli for older ages. Lighter broken lines, fitted by inspection, show estimated limits of variation.

TABLE 7.—*Estimated sizes of bluefin tuna during the summer for ages 0–10 years*

From figure 17

Age in years	Length				Weight in pounds	
	Centimeters (straight)		Inches (curved)			
	Average	Range	Average	Range	Average	Range
0	32	22–43	13.0	9–18	1.5	0.6–3.5
I	57	50–66	23.5	20–27	8.5	5–13
II	77	66–88	31.5	27–36	22.0	14–30
III	95	83–109	39.0	34–45	40	25–50
IV	114	102–127	47.0	42–52	69	45–90
V	133	122–148	55.0	50–61	100	80–140
VI	149	134–165	61.5	55–68	140	105–190
VII	163	148–182	67.0	61–75	185	140–250
VIII	177	161–197	73.0	66–81	240	180–320
IX	190	172–210	78.0	71–86	290	220–395
X	201	182–221	82.5	75–91	340	255–455

Our growth data for fish up to 10 years of age are in good agreement with those of Sella (1929) for Mediterranean bluefin tuna. Our few readings for older ages indicated somewhat larger sizes for western Atlantic fish for the respective ages. Sella's work was based on a larger sample than ours, and he used special instruments which we did not have. Therefore this apparent difference may result from less complete sampling and less precise reading of annuli for the western Atlantic bluefin, rather than to an actual difference in the growth of the larger fish from the respective areas.

LITERATURE CITED

AIKAWA, HIROAKI, and M. KATO.
1938. Age determination of fish (Preliminary Rept. 1). Bull. Japanese Society Scientific Fisheries, vol. 7, No. 1, pp. 79–88. Translation from the Japanese by W. G. Van Campen in U.S. Department of the Interior, Fish and Wildlife Service, Special Scientific Report—Fisheries No. 21.

ARNOLD, EDGAR L., JR.
1951. An impression method for preparing fish scales for age and growth analysis. U.S. Department of the Interior, Fish and Wildlife Service, Progressive Fish Culturist, vol. 13, pp. 11–16.

BULLIS, HARVEY R., JR., and F. J. MATHER, III.
1956. Tunas of the genus *Thunnus* of the northern Caribbean. American Museum Novitates, No. 1765, pp. 1–12.

CONSEIL INTERNATIONAL POUR L'EXPLORATION DE LA MER.
1933. Conference d'experts pour l'examen des méthodes scientifiques et techniques à appliquer à l'étude des poissons de la famille des thonidés. Conseil International pour l'Exploration de la Mer, Rapports et Procès-Verbaux, vol. 84, pp. 91–103.

GALTSOFF, PAUL S.
1952. Staining of growth rings in the vertebrae of tuna (*Thunnus thynnus*). Copeia, No. 2, pp. 103–105.

MOORE, HARVEY L.
1951. Estimation of age and growth of yellowfin tuna (*Neothunnus macropterus*) in Hawaiian waters by size frequencies. U.S. Department of the Interior, Fish and Wildlife Service, Fishery Bulletin, No. 65, vol. 52, pp. 133–149.

PARTLO, J. M.
1955. Distribution, age and growth of eastern Pacific albacore (*Thunnus alalunga* Gmelin). Journal of the Fisheries Research Board of Canada, vol. 12, pp. 35–60.

POSTEL, E.
1954. La croissance du thon á nageoires jaunes *Neothunnus albacora* (Lowe) dans l'Atlantique tropical. Bulletin de la Société Zoologique de France, vol. 79, No. 2–3, pp. 85–90.

RIVAS, LUIS RENE.
1954. A preliminary report on the spawning of the western North Atlantic bluefin tuna (*Thunnus thynnus*) in the Straits of Florida. Bulletin of Marine Science of the Gulf and Caribbean, vol. 4, pp. 302–322.

SELLA, MASSIMO.
1929. Migrazioni e habitat del tonno (*Thunnus thynnus* L.) studiati col metodo degli ami, con osservazioni su l'accrescimento, sul regime delle tonnare ecc. R. Comitato Talassografico Italiano.

SELLA, MASSIMO.
Mem. 156, pp. 3–24. Translation in U.S. Department of the Interior, Fish and Wildlife Service, Special Scientific Report—Fisheries No. 76.

WALFORD, LIONEL A.
1946. A new graphic method of describing the growth of animals. Biological Bulletin, vol. 90, pp. 141–147.

WESTMAN, J. R., and P. W. GILBERT.
1941. Notes on age determination and growth of the Atlantic bluefin tuna, *Thunnus thynnus* (Linnaeus). Copeia, No. 2, pp. 70–72.

WESTMAN, JAMES R., and W. C. NEVILLE.
1942. The tuna fishery of Long Island, New York. Board of Supervisors, Nassau County, Long Island, N.Y., pp. 1–31.

UNITED STATES DEPARTMENT OF THE INTERIOR, Fred A. Seaton, *Secretary*
FISH AND WILDLIFE SERVICE, Arnie J. Suomela, *Commissioner*
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FECUNDITY OF RED SALMON AT BROOKS AND KARLUK LAKES, ALASKA

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ABSTRACT

The relation between mideye-fork length and number of eggs for red salmon at Brooks Lake (1957–58) and Karluk Lake (1958) is established. A review of available literature on fecundity at Karluk Lake indicates that there may have been a long-term decrease in the size of females and correspondingly in the average number of eggs per female.

Annual variations in age composition by life-history categories and in sex ratios affect the number of eggs available for deposition. Analyses of Karluk Lake red salmon stocks show a relation between the ocean age and size of fish and their fecundity, those fish of a greater length of ocean residence and size having the largest number of eggs. Since a distinctive seasonal pattern in the occurrence of life-history categories and related sex ratios exists, it is theorized that the commercial fishery could be so concentrated as to deplete that portion of the run of highest egg production potential.

FECUNDITY OF RED SALMON AT BROOKS AND KARLUK LAKES, ALASKA

BY WILBUR L. HARTMAN AND CHARLES Y. CONKLE, *Fishery Research Biologists*
BUREAU OF COMMERCIAL FISHERIES

Fecundity of red salmon, *Oncorhynchus nerka* (Walbaum), was studied at Brooks and Karluk Lakes, Alaska, for use in estimating the reproductive potential of spawning stocks. Reproductive potential is defined here as the total number of eggs available for seeding in a particular spawning population. Such information forms the basis for determining survival rates of red salmon during various life-history stages in fresh water.

Adult red salmon enter Brooks Lake by way of Bristol Bay and Naknek River, and enter Karluk Lake by way of Shelikof Strait and Karluk River (fig. 1). The Bureau of Commercial Fisheries maintains research stations at both lakes to investigate factors responsible for fluctuations in the abundance of salmon runs that have occurred in these areas (U.S. Fish and Wildlife Service, 1958). Certain specific problems differ between the lakes, but all research is integrated into a broad study of the physical, chemical, and biological factors affecting the fresh-water survival of red salmon.

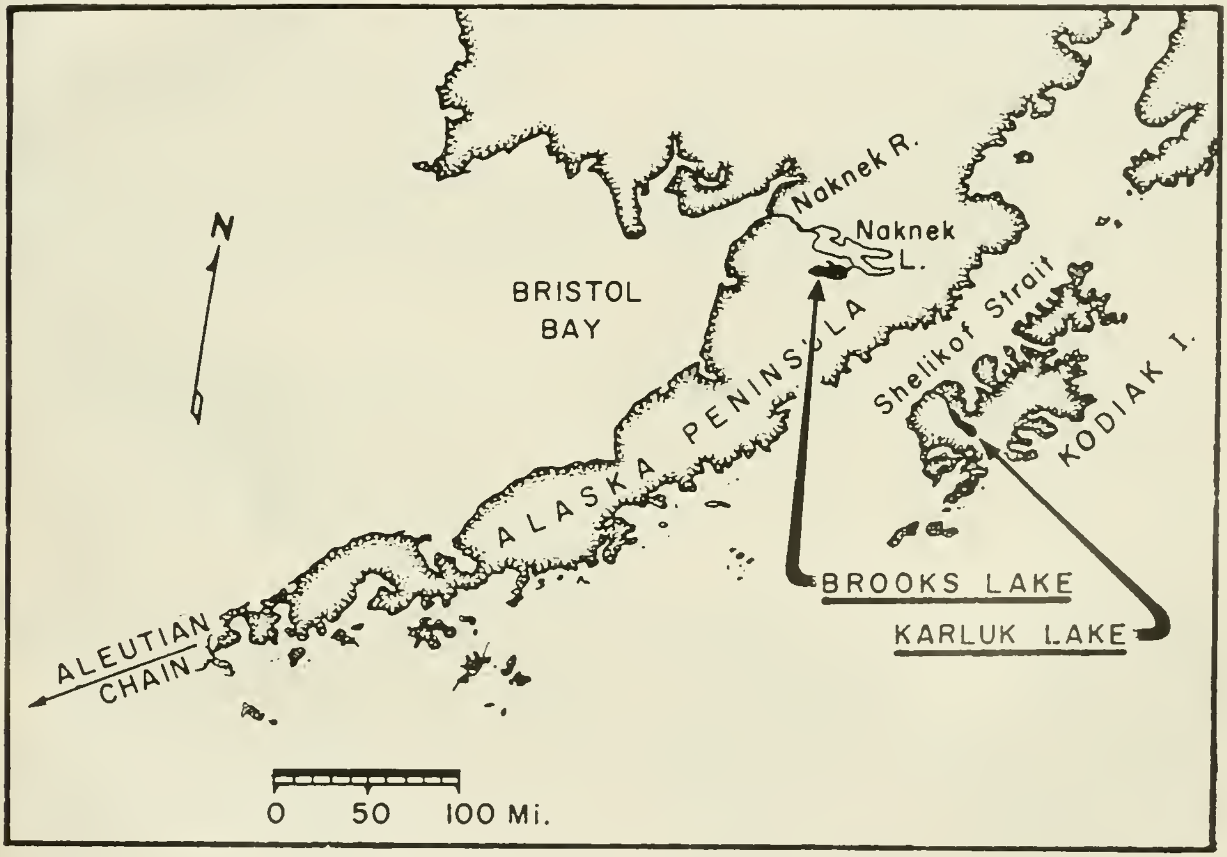

FIGURE 1.—Brooks and Karluk Lakes in western Alaska.

Red salmon were sampled from spawning migrations into Brooks Lake in 1957 and 1958, and into Karluk Lake in 1958. Earlier data are avail-

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NOTE.—Approved for publication, Jan. 13, 1960. Fishery Bulletin 180.

able for Karluk Lake and are used for comparison in the discussion that follows.

We wish to express our thanks to Allen McCready, William Pogue, and Patrick Tomlinson for aid in developing and conducting field operations, and to Theodore R. Merrell and John B. Owen of the Bureau of Commercial Fisheries, for reviewing the manuscript.

COLLECTION AND TREATMENT OF MATERIALS

Ovaries used in these studies were obtained from females trapped at adult immigration sites at both lakes. They were taken throughout the season and over the size range of females in the stocks. A few females killed during beach-seining and gill-netting operations in Brooks Lake were also used. Only females not fully ripe were examined. This reduced the possibility of including partially spawned females.

Both ovaries were removed intact and placed in 20-percent formalin. An identification tag was attached to the right ovary to distinguish it from the left. After hardening for at least 48 hours, ovaries were removed from the formalin and thoroughly washed in water. The eggs were stripped from the ovarian tissue by hand and also thoroughly washed in water. Total numbers of eggs were counted in each ovary of each female sampled at both lakes. A mechanical hand tally was used.

Sampling methods involving volume or weight were experimented with at Brooks Lake in 1958. The most reliable method was to extract 3 random 100-egg samples from each gonad and estimate the total count from the average count-weight relation of the selected samples. Fecundity was usually estimated within 2 percent of the actual count. This method is sufficiently accurate and should be considered where extensive fecundity studies are scheduled.

RELATION BETWEEN SIZE OF FISH AND FECUNDITY

A relation exists between the size of fish and the number of eggs in the body cavity. Ricker (1932) shows that the relation between fish length and egg count in brook trout (*Salvelinus fontin-*

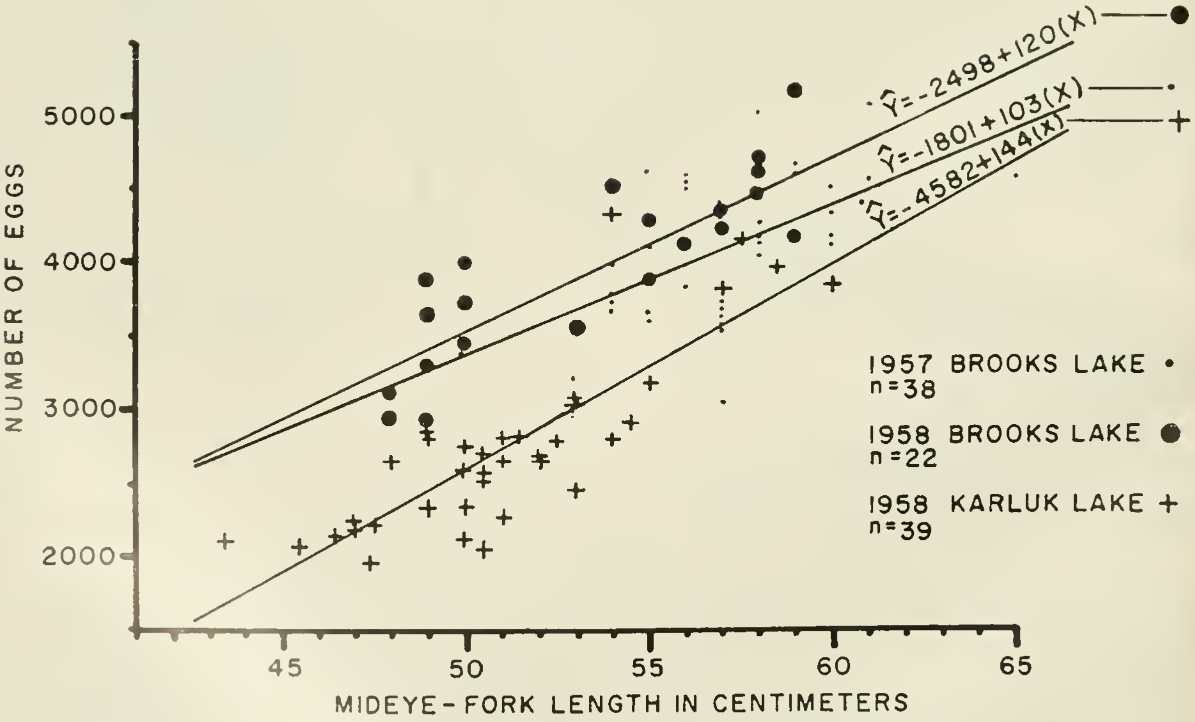

FIGURE 2. Relation of egg counts to mideye-fork length for red salmon at Brooks Lake, 1957 and 1958, and at Karluk Lake, 1958.

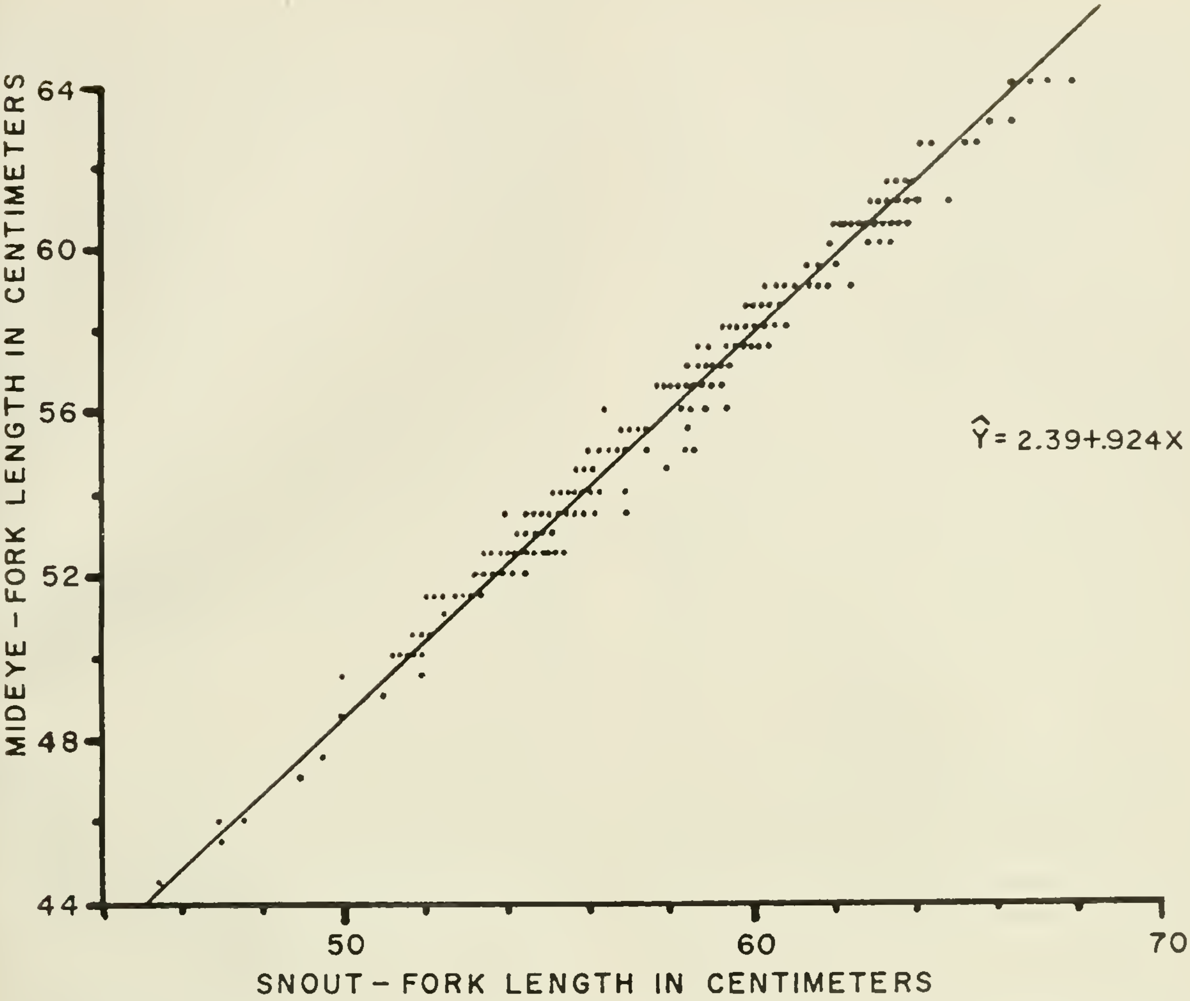

FIGURE 3.—Relation of snout-fork length to mideye-fork length for 193 female red salmon sampled in the Karluk River, 1952.

alis) is curvilinear. Rounsefell (1957) states that over the narrower ranges of length at maturity found in *Oncorhynchus* sp., the straight-line equation adequately describes the relationship. This view was held earlier for red salmon by Foerster and Pritchard (1941). They believed that the overall relation between fish length and number of eggs was probably logarithmic, but since adult spawning red salmon generally fall within a limited size range, the straight-line equation was adequate.

Total egg counts for females examined at Brooks and Karluk Lakes are plotted against mideye-fork length in figure 2. Linear regression equations were derived for these sets of data by the method of least squares.

Since fecundity studies at Karluk Lake have involved various length measurements, lengths in this paper represent transformations to mideye-fork lengths from data given in figure 3. The mideye-fork length is measured along the side of the fish from the center of the eye socket to the fork in the tail. This length was first used in Alaska by the Fisheries Research Institute of the University of Washington. It avoids the variability in total lengths associated with changes in the appearance of the skull during development of secondary sexual characteristics among most spawning salmonids.

The earliest recorded study of fecundity at Karluk Lake was conducted by Chamberlain (1907) who obtained a mean egg count of 3,500 per fish. In 1926, Smith (in: Gilbert and Rich, 1927) examined ovaries from 40 females and observed a mean fecundity of 3,728 eggs and a mean mideye-fork length of 56.4 centimeters. A mean fecundity of 3,237 eggs and a mean length of 55.4 cm. are derived from data given by Rounsefell (1957) for 411 females examined from 1938 to 1941. The average length of female red salmon in the 1958 escapement at Karluk Lake was 51 cm., and the average fecundity was 2,762 eggs.

These data suggest a long-term decrease in size and fecundity of red salmon at Karluk Lake that may be real and thus an important consideration in the declining abundance of that stock. This indication of a downward trend in size and fecundity may also be due to sampling inadequacies. The 40 fish studied by Gilbert and Rich (1927) were collected on a single day, September 15, 1926. The 411 fish included in the analysis by Rounsefell (1957) were taken chiefly from the spring portion of the run. As we shall see in a later section, age and size composition of the run changes during the season. Therefore, differences in mean size and fecundity may reflect differences within seasons as well as between seasons.

Recent data on red salmon in Alaska show that lengths and fecundity vary considerably. Mathisen (1955) [1] found for 1948 and 1950–52 that the mean mideye-fork length of females at Pick Creek (a tributary of Lake Nerka in the Bristol Bay area) was 53.0 cm., and the average fecundity was 4,011 eggs. Average lengths and fecundities at Brooks Lake for 1957 were 55.5 cm. and 3,916 eggs, and for 1958 were 53.3 cm. and 3,898 eggs. Average length was 51 cm., and average fecundity was 2,762 eggs for 1958 at Karluk Lake.

These differences are not due exclusively to variations in fish sizes between years or stocks. Real differences in fecundity for fish of the same size are shown by Rounsefell (1957) and are clearly evident between Brooks and Karluk Lakes stocks (fig. 2).

VARIATION BETWEEN PAIRED OVARIES

Although the maturation rates are the same for eggs in the left and right ovaries (Rounsefell, 1957), the number of eggs in each side is usually different. Brown and Kamp (1942) state that in brown trout (*Salmo trutta*) the posterior portion of the intestine usually bends to the right, crowding the right ovary at its posterior end and making it smaller than the left. No bend in the intestine was detected in brown trout with ovaries of the same size.

Egg counts for left ovaries were plotted against those of the corresponding right ovaries for 1957 and 1958 samples at Brooks Lake and for 1958 samples at Karluk Lake (fig. 4). Ninety percent of the left ovaries held more eggs than the right in 1957 Brooks Lake samples, 91 percent in 1958 Brooks Lake samples, and 69 percent in the 1958 Karluk Lake samples. Red salmon at Bare Lake on Kodiak Island have the opposite condition, more eggs in the right ovary than in the left (Nelson, 1959). Karluk Lake data are consistent with Rounsefell's (1957) findings in 1939, in which the number of eggs in ovaries from small fish was similar between right and left sides; but as the total number of eggs increased, the proportion in the left ovary became increasingly greater than in the right.

REPRODUCTIVE POTENTIAL OF SPAWNING POPULATIONS

The number of salmon spawning in a locality is often regarded as indicative of the reproductive potential. Escapement figures have been used since the inception of management of our salmon resources to predict the strength of future runs. However, considerable variability in the reproductive potential may actually exist independent of the actual number of spawners.

Annual differences in sex ratios alone can cause substantial differences in the number of eggs available for deposition. Average fecundity for female red salmon was relatively stable during three years at Babine Lake (Withler, 1950), but a high preponderance of males in one of these years reduced by one-half the reproductive potential of that spawning population, even though the

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[1] Studies on the spawning biology of the red salmon, *Oncorhynchus nerka* (Walbaum), in Bristol Bay, Alaska, with special reference to the effect of altered sex ratios. Ole A. Mathisen, doctoral dissertation, University of Washington.

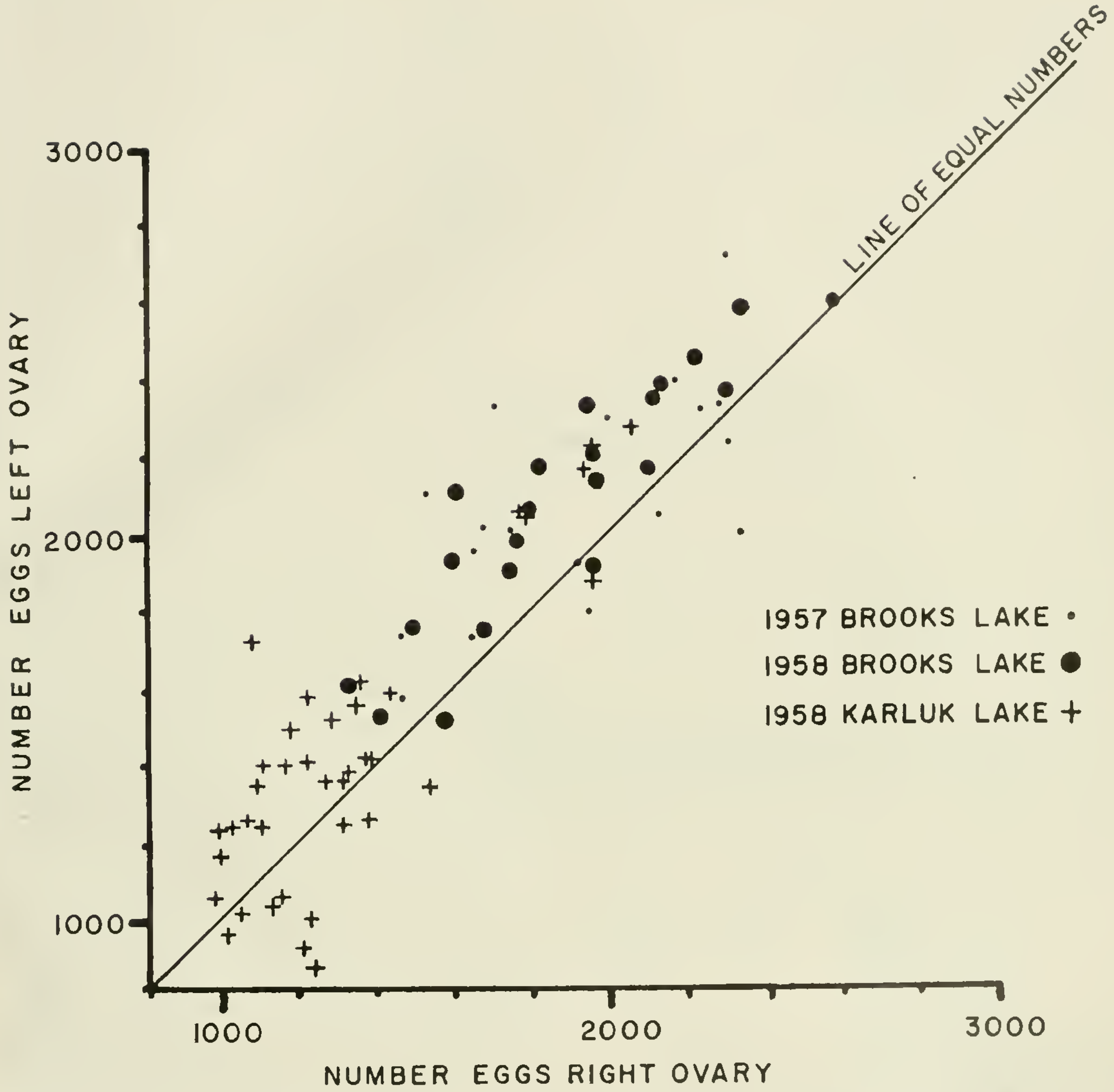

Figure 4.—Egg counts for right and left ovaries of female red salmon sampled at Brooks Lake, 1957 and 1958, and Karluk Lake, 1958.

number of spawners was approximately the same (table 1). Mathisen [2] in a study of egg mortality as related to sex ratio differences concludes that in red salmon, mortality of eggs was only slightly higher with a sex ratio as high as 15 females to 1 male than with a ratio of 1 to 1. Thus, even a highly unbalanced spawning stock favoring females may result in only minor decreases in ultimate egg survival from each female. Such a stock might yield a considerable increase in potential production over stocks of the same size, but with more evenly balanced sex ratios.

Table 1.—*Reproductive potential of red salmon at Babine Lake in 1946, 1947, and 1949 (after Withler, 1950)*

Item	1946	1947	1949
Total number of red salmon	475,419	522,561	509,132
Estimated number of females	237,500	151,020	270,451
Potential egg deposition	736,000,000	461,500,000	916,600,000

---

[2] See footnote 1.

Variability in life-history categories among females can be the cause of considerable change in reproductive potential from year to year, even though the number of spawners and sex ratio remain constant. Life-history categories are defined as groups of fish with different combinations of fresh-water- and ocean-years of life and are denoted by 2 figures; for instance, 5_3 denotes fish that migrated to the ocean in their third year of life and returned to spawn in their fifth year. Analysis of the Karluk Lake age data in 1958 shows that 2 major categories dominate the spawning populations, 5_3 and 6_4 (table 2). However, in some years one or more other age categories contribute considerable numbers of fish to the run. The salient feature of this population structure (table 2) is the great difference in the length and fecundity relation between life-history categories with 1, 2, and 3 years of ocean life; i.e., 4_3 and 5_4 versus 5_3 and 6_4 versus 6_3 and 7_4. Marked annual differences in the abundance of 1-ocean-year, 2-ocean-year, or 3-ocean-year fish could substantially alter the reproductive potential.

TABLE 2.—*Reproductive potential of the 1958 escapement at Karluk Lake by life-history categories*

Life history category	Number of females [1]	Mean length (cm.) [2]	Mean fecundity [3]	Potential egg deposition
4_3	814	43.5	1,674	1,363,000
5_4	2,471	43.8	1,717	4,243,000
5_3	60,872	51.4	2,810	171,050,000
6_4	53,601	51.3	2,796	149,868,000
6_3	8,695	54 3	3,227	28,059,000
7_4	2,186	53.8	3,155	6,897,000
Total [4] ----	--------------	--------------	--------------	361,480,000

[1] Based on a sample of 2,108 red salmon from the 1958 escapement.

[2] Mideye-fork length.

[3] Determined by substituting mean lengths into the fecundity equation (fig. 2).

[4] The very minor categories, 4_2, 6_5, and 7_5, contribute an estimated 1,000,000 eggs to the potential egg deposition.

Sex ratios for each life-history category must be considered in any study of the reproductive potential of spawning populations. Barnaby (1944) shows that the sex ratio of the Karluk Lake spawning populations varied considerably when important life-history categories varied in dominance. He found over several years that the average proportion of males in the 1-ocean-year categories (4_3 and 5_4) ranged from 100 to 75 percent, the 2-ocean-year categories (5_3 and 6_4) ranged from 62 to 32 percent, and the 3-ocean-year categories ranged from 38 to 35 percent.

The reproductive potential and the egg contribution from each of the six major life-history categories comprising the 1958 run at Karluk Lake is shown in figure 5. Examination of these data indicates that 89 percent of the eggs for potential deposition came from the two 2-ocean-year categories, 5_3 and 6_4.

Barnaby (1944) shows that a seasonal pattern of appearance of the different life-history categories exists at Karluk Lake. As the daily composition of the run changes throughout the season, obviously so does the reproductive potential. It is possible that the commercial fishery could have been concentrated during that seasonal time of migration when important groups such as the 5_3 and 6_4 categories were moving through the fishing grounds. As a result, the reproductive potential of the spawning populations could be seriously reduced because of a shift in age composition to younger ocean-age groups. These fish on a one-for-one basis are less fecund. It is interesting that the 3-ocean-year categories (6_3 and 7_4) accounted for only about 6 percent of the 1958 escapement, which is the lowest contribution by these groups ever recorded (Rounsefell, 1958: 156). At the same time the 1-ocean-year categories (4_3 and 5_4) accounted for 17 percent of the 1954 escapement, which is by several times the highest contribution from those categories ever recorded. Analysis of future Karluk escapements will determine if this substantial shift in ocean-age composition is the result of a real trend or merely variability in year-class strength.

It is concluded that a detailed study of the reproductive potential of the spawning populations is necessary to establish a basis for fresh-water survival studies of red salmon. It may also serve to help explain, at least in part, the causes for declines in red salmon runs over the past decades.

SUMMARY

The relation between egg count and mideye-fork length was derived for Brooks and Karluk Lakes red salmon. Comparing recent Karluk Lake data with past fecundity studies indicates that a long-term decrease in mean size and fecundity of females has occurred.

Red salmon at Brooks and Karluk Lakes consistently had more eggs in the left ovary than in the right.

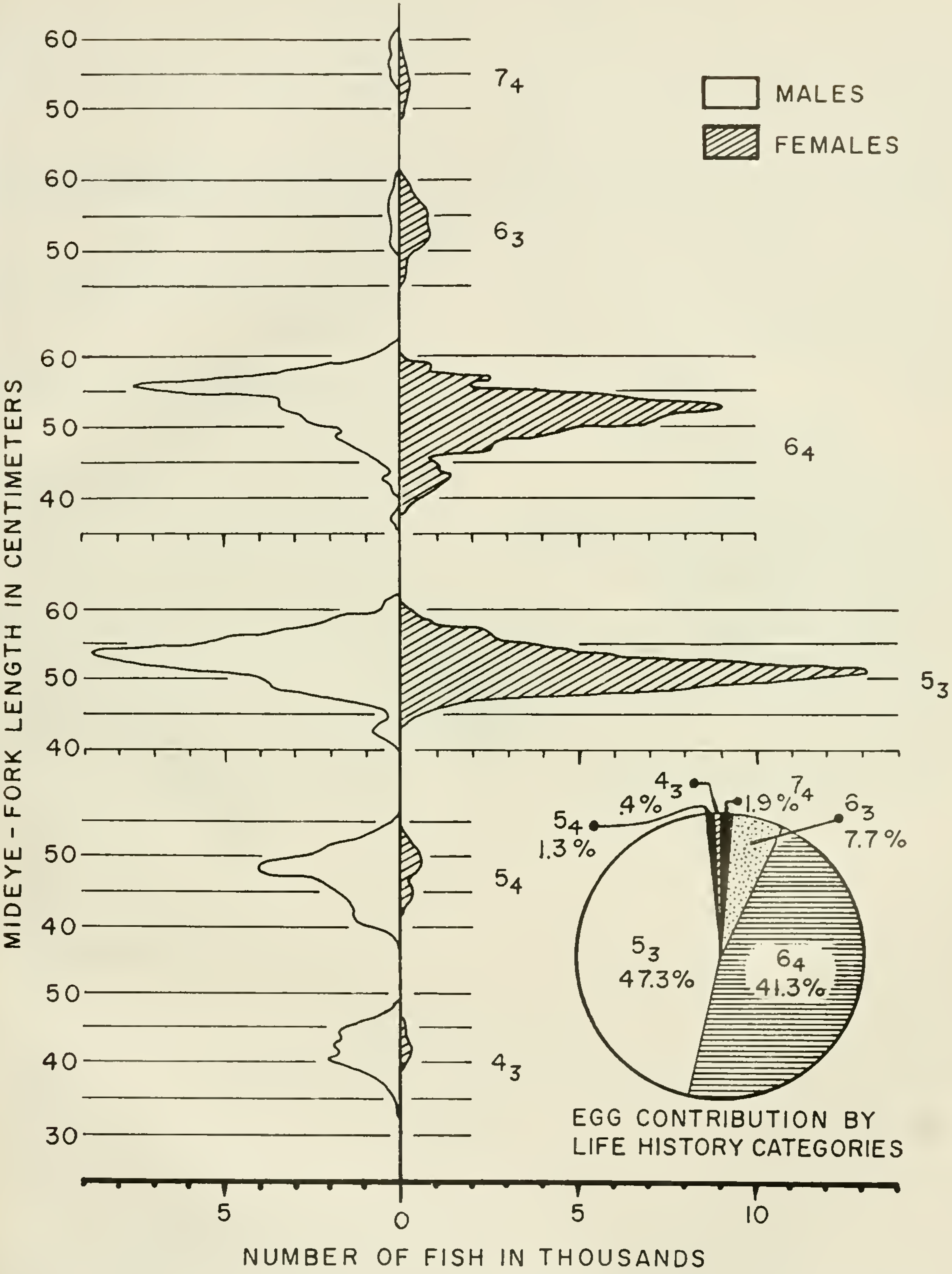

FIGURE 5.—Length-frequency distributions and reproductive potential by life-history categories of the escapement at Karluk Lake, 1958.

Variability in the reproductive potential of spawning stocks was shown to be attributable to at least 4 factors: (1) biological differences in fecundity between fish of the same size, (2) change in the life-history composition of spawning stocks, (3) differences in sex ratios between life-history categories, and (4) seasonal differences in reproductive potential evidenced from the well defined pattern of occurrence by life-history categories at Karluk Lake.

The possibility of the commercial fishery being concentrated on the most fecund life-history categories is theorized as a contributing factor to the declines in red salmon runs over the past several decades.

LITERATURE CITED

Barnaby, Joseph T.

1944. Fluctuations in abundance of red salmon, *Oncorhynchus nerka* (Walbaum), of the Karluk River, Alaska. Fishery Bulletin, U.S. Fish and Wildlife Service, vol. 50, No. 39, pp. 237–295.

Brown, C. J. D., and Gertrude C. Kamp.

1942. Gonad measurements and egg counts of brown trout (*Salmo trutta*) from the Madison River, Montana. Transactions of the American Fisheries Society, vol. 71, pp. 195–200.

Chamberlain, F. M.

1907. Some observations on salmon and trout in Alaska. Report Commissioner of Fisheries for 1906. Bureau of Fisheries Document 627, 112 pp.

Foerster, R. Earle, and Andrew L. Pritchard.

1941. Observations on the relation of egg content to total length and weight in the sockeye salmon (*Oncorhynchus nerka*) and the pink salmon (*O. gorbuscha*). Transaction Royal Society of Canada 35, sec. V:51–60.

Gilbert, Charles H., and Willis H. Rich.

1927. Investigations concerning the red-salmon runs to the Karluk River, Alaska. Bulletin U. S. Bureau of Fisheries, vol. 43, pt. 2, pp. 1–69.

Nelson, Philip R.

1959. Effects of fertilizing Bare Lake, Alaska, on growth and production of red salmon (*O. nerka*). Fishery Bulletin, U.S. Fish and Wildlife Service, vol. 60, No. 159, pp. 59–86.

Ricker, William E.

1932. Studies of speckled trout (*Salvelinus fontinalis*) in Ontario. Publications Ontario Fisheries Research Laboratory, No. 44, pp. 67–110. *In* University of Toronto Studies, Biol. Ser. No. 36.

Rounsefell, George A.

1957. Fecundity of North American Salmonidae. Fishery Bulletin, U.S. Fish and Wildlife Service, vol. 57, No. 122, pp. 451–468.

1958. Factors causing decline in sockeye salmon of Karluk River, Alaska. Fishery Bulletin, U.S. Fish and Wildlife Service, vol. 58, No. 130, pp. 83–169.

U.S. Fish and Wildlife Service.

1958. Progress report on Alaska fisheries management and research for 1957. U.S. Fish and Wildlife Service, Special Scientific Report–Fisheries No. 258, 22 pp.

Withler, F. C.

1950. Egg content of Babine sockeye. Fisheries Research Board of Canada, Progress Reports, Pacific Coast Station, No. 82, pp. 16–17.

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FISH AND WILDLIFE SERVICE
Bureau of Commercial Fisheries, Donald L. McKernan, *Director*

FILEFISHES (MONACANTHIDAE) OF THE WESTERN NORTH ATLANTIC

By Frederick H. Berry and Louis E. Vogele

MARINE BIOLOGICAL LABORATORY

March 3, 1849

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ABSTRACT

Filefishes of the western North Atlantic, important forage fish because of their abundance, have been inadequately described and are difficult to identify to species. In determining the species that occur in the western North Atlantic, several thousands of young and adult specimens were examined, and four genera and nine species were found to be valid and separable by external characters: *Alutera monoceros*, *A. scripta*, *A. schoepfii*, *A. heudelotii*, *Monacanthus ciliatus*, *M. tuckeri*, *Stephanolepis hispidus*, *S. setifer*, and *Amanses pullus*.

Considerable intraspecific variation in profile was found, resulting in the synonymizing of several species, among them *Alutera punctata* and *Stephanolepis spilonotus*.

Evidence is presented for the use of Monacanthidae as the family name, rather than Aluteridae.

Keys to juvenile and adult specimens are presented, and proportional measurements and fin-ray counts are given in tabular form. Graphs, charts, photographs, and drawings supplement the data to facilitate identification.

Information on ranges and behavior is also presented.

FILEFISHES (MONACANTHIDAE) OF THE WESTERN NORTH ATLANTIC

By Frederick H. Berry and Louis E. Voegle, *Fishery Research Biologists*

Bureau of Commercial Fisheries

Filefishes of the family Monacanthidae that occur in the western North Atlantic Ocean have been studied as a part of the biological research program of the United States Bureau of Commercial Fisheries Biological Laboratory at Brunswick, Georgia. This program is concerned with an evaluation of the fauna off the southeastern Atlantic coast of the United States. However, the study of the filefishes, because of their wide distribution, was not limited to this area. Several of the species concerned may occur north to Newfoundland and south to Brazil, and two of them probably have a worldwide distribution.

Examination of collections made in recent years—during cruises of the M/V *Theodore N. Gill*, *Oregon*, *Combat*, and *Silver Bay* off the south Atlantic coast of the United States—by dip net, plankton tows, meter larvae net, and from stomach contents of larger fish taken by trolling, has indicated that the filefishes are a numerically abundant group and comprise an important part of the planktonic and forage-fish fauna. Recent catches at trawling stations in this area have furnished additional specimens for taxonomic, morphological, and environmental evaluation. Many of these specimens are in the collection of the Brunswick Biological Laboratory, but several museum and university collections of filefishes were examined to augment this material.

Nine species of filefishes from the western North Atlantic were identified—primarily from specimens taken off the United States. These species are *Alutera monoceros* (Linnaeus), *Alutera scripta* (Osbeck), *Alutera schoepfii* (Walbaum), *Alutera heudelotii* Hollard, *Monacanthus tuckeri* Bean, *Monacanthus ciliatus* (Mitchill), *Stephanolepis hispidus* (Linnaeus), *Stephanolepis setifer* (Bennett), and *Amanses pullus* (Ranzani).

It is our purpose to give reasons for use of these names, to briefly diagnose and distinguish the genera and species, to furnish illustrations of the species, and to list the specimens examined that they shall be readily available for more detailed future studies.

In accomplishing these objectives we have determined several aspects of the life histories of these fishes, added to the knowledge of their distribution, discovered and confirmed certain anatomical features, described morphological and meristic variation, and through our own studies and from published accounts we have summarized their taxonomic relationships. We have been dogmatic in our taxonomic pronouncements concerning the several taxonomic problems that remain in order to stabilize the nomenclature until adequate numbers of specimens from the entire geographical ranges of these groups can be studied. We have explained the problems involved.

Previously, the two most useful references for identifying specimens of Monacanthidae from the western North Atlantic were publications by Fraser-Brunner (1940, 1941).

We have found that the early life-history stages of the Atlantic coast species occur pelagically in offshore waters, and believe these waters probably are the principal habitat for those stages. The late juvenile and adult stages tend to adopt inshore or benthic–offshore habitats. Preliminary inspection of the extensive plankton collections made off the coasts of North and South Carolina, Georgia, and east Florida by the *Gill* in 1953–54 (see Anderson, Gehringer, and Cohen, 1956) has indicated that larval filefish are relatively abundant in waters of the Gulf Stream in this area. Samples taken by dip net on the *Gill* and other vessels have indicated the abundance of juvenile specimens in offshore waters, particularly in association with floating seaweed. Although juveniles are taken in inshore waters and are seined on the beaches, the specimens from offshore waters appear to be more abundant and of a smaller average size. Available data

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on larger juveniles and adults show that they were usually taken from or near the bottom in shallow waters out to depths of about 25 fathoms. We have heard reports of large specimens of *Alutera* floating at the surface far out at sea, and we have also been told that these and large specimens of other filefish genera have been seen by skin divers on or near the bottom. All of the large specimens on which we have adequate collection data were taken by bottom-collection methods.

We are indebted to the following persons for making specimens available that were instrumental in this study: James E. Böhlke, Academy of Natural Sciences of Philadelphia; Eugenie Clark, Cape Haze Marine Laboratory; Earl E. Deubler, Jr., University of North Carolina; W. I. Follett, California Academy of Sciences; John D. Kilby, University of Florida; George S. Myers, Stanford University; Leonard P. Schultz, U.S. National Museum; Victor G. Springer, Florida State Board of Conservation; and Royal D. Suttkus, Tulane University. We are grateful for the assistance of the entire staff of the U.S. Bureau of Commercial Fisheries Biological Laboratory at Brunswick.

METHODS

Body measurements greater than about 6 millimeters were taken with dial calipers or with dividers and a metric scale; smaller measurements were taken with a microscope and calibrated micrometer eyepiece. Measurements of less than 100 mm. were generally recorded to the nearest 0.1 mm.; larger measurements, to the nearest millimeter.

Counts of rays of the soft dorsal, anal, and pectoral fins were made with a microscope and transmitted light on all specimens of less than about 250 mm. standard length. Each discernible ray was counted, including the small or rudimentary ray that occasionally is present at the posterior end of the fins. Only the pectoral and caudal fins have branched rays. All species examined have two dorsal spines and one pectoral spine; the second dorsal spine and the pectoral spine become minute or vestigial with growth of the fish. The pectoral spine was not included in the count of that fin. By definition, a ray in a fin may be of two types: a spine (which usually has a pointed tip, is never segmented, and is never branched) and a soft ray (which usually has a blunt or fimbriated tip, is segmented, and may or may not be branched).

Obvious deformities were neither counted nor measured.

The following measurements are illustrated in figures 1 and 2.

Standard length (*S.L.*).—Distance from tip of snout (upper lip) to middle of caudal-fin base. The caudal-fin base is distinguished externally as the curved ridge formed by the proximal ends of the caudal-fin rays. This ridge is not to be confused with the line formed by the extension of body skin and scales onto the bases of the caudal rays. Percent of standard length is recorded as "% S.L."

Body depth.—Distance between origins of second dorsal fin and anal fin.

Head length.—Distance from tip of snout (upper lip) to upper end of gill slit.

Snout length.—Distance from tip of snout (upper lip) to anterior margin of orbit.

Eye diameter (*orbit diameter*).—Horizontal diameter of orbit.

Eye to dorsal spine.—Straight-line distance from top of orbit to front center of base of first dorsal spine.

Dorsal-spine length.—Distance from front center of base of dorsal spine to its tip.

Caudal-fin length.—Distance from middle of caudal base to tip of longest caudal ray.

Peduncle depth.—Least depth of caudal peduncle, a vertical measurement from posterior end of anal-fin base.

Peduncle length.—Shortest distance, from posterior end of anal-fin base to caudal-fin base along ventral surface of peduncle.

IDENTIFICATION

Our dichotomous keys to filefishes of the western North Atlantic have been constructed to allow for intraspecific and interspecific variation, and for ontogenetic changes in form and morphometrics. When our series of specimens was small or incomplete in size range, we attempted to anticipate variation and ontogenetic changes, particularly by not using or qualifying the use of characters that we suspect might not be valid at specimen sizes we did not have.

KEY TO GENERA OF MONACANTHIDAE FROM THE WESTERN NORTH ATLANTIC

A. Pelvic bone without an external spine or with only a very small rudimentary barbed spine present in three species (fig. 5). Gill slit usually very oblique (at an angle of about 45° from longitudinal body axis on specimens larger than 40 mm. S.L.) (fig. 4). First dorsal spine located over middle or back of eye (fig. 4). Anal-fin rays, 35 to 52 (fig. 3) ---------- *Alutera.*

AA. Pelvic bone with a prominent external spine (fig. 5). Gill slit nearly vertical or only slightly oblique (fig. 4) ---- B.

B. A deep groove behind the dorsal spines (fig. 27B). Pelvic spine not movable (fusion may be broken on damaged specimens) (fig. 5). First dorsal spine inserted over anterior part of eye (on specimens 30 mm. S.L. and larger) (fig. 4). Anal-fin rays, 29 to 32 (fig. 3) ---------- *Amanses.*

BB. No deep groove behind the dorsal spines. Pelvic spine movable in anterioposterior direction (fig. 5). First dorsal spine inserted over posterior part of eye (fig. 4). Anal-fin rays, 26 to 36 (fig. 3) ---------- C.

C. Scales with 1 to 8 or more spines, each spine arising individually from the scale base, and none of the spines branched; the spines usually separate but joined basally by a thin bony connection on larger specimens (95 mm. S.L. and larger; fig. 8). Body relatively shallower (table 12). Caudal peduncle of specimens 20 mm. S.L. and larger with 2 to 4 pairs of enlarged spines on each side (spines recurved in males). No elongated dorsal rays. Ventral flap relatively large (fig. 30) ---------- *Monacanthus.*

CC. Scales usually with 1 spine, but with about 3 to 8 closely joined spines in larger specimens (100 mm. S.L. and larger). On specimens larger than about 40 mm. S.L. the spines branched one to many times above their bases; on specimens between about 19 and 40 mm. S.L. the spines of only a part of the scales are branched; and on specimens smaller than about 19 mm. S.L. spines are not branched (fig. 8). Body relatively deeper (table 12). No enlarged paired and recurved spines on caudal peduncle. Second dorsal ray elongated in mature males. Ventral flap relatively small (fig. 31) ---------- *Stephanolepis.*

KEYS TO SPECIES OF MONACANTHIDAE FROM THE WESTERN NORTH ATLANTIC

Genus *Alutera* Cloquet

A. Dorsal rays 43 to 50. Anal rays 46 to 52 (fig. 3). Pectoral rays modally 14 ---------- B.

B. Caudal peduncle longer than deep; peduncle length into peduncle depth 0.65 to 0.95 times. Caudal fin relatively short, about 18 to 26% S.L. Eye to dorsal spine distance relatively large, 7.0 to 8.6% S.L. Depth relatively great on specimens smaller than 175 mm. S.L., 36.8 to 43.8% S.L. (fig. 35) ---------- *Alutera monoceros.*

BB. Caudal peduncle deeper than long on specimens larger than 30 mm. S.L.; peduncle length into peduncle depth 1.24 to 1.60 times on specimens larger than 50 mm. S.L., 1.03 to 1.05 times on specimens of 31 to 46 mm. S.L., 0.86 on a 27-mm. specimen. Caudal fin relatively long, about 33 to 61% S.L. Eye to dorsal spine distance relatively small, 5.0 to 6.7% S.L. Depth relatively shallow on specimens smaller than 175 mm. S.L., 21.5 to 33.1% S.L. (fig. 35) ---------- *Alutera scripta.*

AA. Dorsal rays 32 to 41. Anal rays 35 to 44 (fig. 3). Pectoral rays modally 12 and 13 ---------- C.

C. No pelvic spine. Eye to dorsal spine distance variable and relatively large on specimens larger than 100 mm. S.L. (fig. 34), 7.3 to 13.5% S.L. Eye relatively small on specimens larger than 175 mm. S.L., 4.8 to 6.8% S.L. Body depth relatively small in specimens smaller than 35 mm. S.L., 17.3 to 23.2% S.L. Snout relatively short on specimens smaller than 45 mm. S.L., 12.0 to 23.9% S.L. Body scales relatively large and sparse; spines on scales relatively long and not close set (fig. 6), producing a comparatively rough feeling to the touch. Dorsal spine relatively long, thin, and with small barbs (fig. 7). Ventral profile of specimens smaller than about 45 mm. S.L. flatly curved, not produced into an angle (fig. 11). Pigment pattern of preserved specimens of about 70 to 200 mm. S.L., usually consisting of relatively fewer rounded spots or stripes mainly present on the ventral portion of the body; however, this pigmentation may be entirely absent (fig. 23). Coloration of live specimens with few to many orange spots ---------- *Alutera schoepfii.*

CC. Rudimentary pelvic spine present (on specimens 30 to 135 mm. S.L.) (figs. 4 and 5). Eye to dorsal spine distance relatively small on specimens larger than 100 mm. S.L. (fig. 34), 4.6 to 6.6% S.L. Eye relatively large on specimens larger than 175 mm. S.L., 6.2 to 7.7% S.L. Body depth relatively great in specimens smaller than 35 mm. S.L., 27.6 to 30.6% S.L. Snout relatively long on specimens smaller than 45 mm. S.L., 23.8 to 26.7% S.L. Body scales relatively small and numerous; spines on scales relatively short and close set (fig. 6), producing a "velvety" feeling to the touch, especially on specimens larger than 70 mm. S.L. Dorsal spine relatively short with large barbs (fig. 7); this condition pronounced on specimens between 40 and 140 mm. S.L. Ventral profile on specimens smaller than about 45 mm. S.L. produced in a convex angle by the extended pelvic bone (fig. 12). Pigment pattern of preserved specimens larger than about 70 mm. S.L. consisting of rounded or elongated and rounded spots, these more numerous on the dorsal half of the body (fig. 25). Color markings on live specimens bluish purple ---------- *Alutera heudelotii.*

Genus *Monacanthus* Oken

A. Body depth relatively shallow, 31.3 to 38.6% S.L. (fig. 36). Head relatively long on specimens larger than 40 mm. S.L., 33.1 to 36.1% S.L. Snout relatively long on specimens larger than 30 mm. S.L., 25.4 to 28.1% S.L.---------- *Monacanthus tuckeri.*

AA. Body depth relatively great, 39.1 to 54.5% S.L. (fig. 36). Head relatively short on specimens larger than 40 mm. S.L., 29.0 to 33.3% S.L. Snout relatively short on specimens larger than 30 mm. S.L., 21.9 to 25.7% S.L.---------- *Monacanthus ciliatus.*

Genus *Stephanolepis* Gill

A. Dorsal rays usually 31 to 34, rarely 29, 30, or 35. Anal rays usually 31 to 34, rarely 30 or 35 (table 10). Pigment pattern of preserved specimens between about 27 and 65 mm. S.L. consisting of a longitudinal arrangement of relatively few, small, dark dashes in several rows and several relatively large, dark, oblique or vertical blotches on the sides; the breast and snout without small flecks of pigment; and two moderately distinct dusky bars of about equal intensity on the caudal fin (fig. 31). On larger specimens the body dashes and caudal bars tend to become indistinct, the blotches on the sides become larger and more irregular, and the breast and snout become generally darker, but still lack a spotted effect [1]---------- *Stephanolepis hispidus.*

AA. Dorsal rays usually 27 to 29, rarely 30. Anal rays usually 27 to 29, rarely 26 or 30 (table 10). Pigment pattern of preserved specimens between about 27 and 65 mm. S.L. consisting of a relatively greater number of rows of dark dashes (which are more sharply defined and which give a broken-lines effect to the sides) and relatively small vertical or oblique blotches present on the sides; the breast and snout with few to many small flecks or spots of pigment; and two very distinct bars on the caudal fin, the anterior bar the darker (fig. 31). On larger specimens the body dashes and blotches and the caudal bars are less distinct, but the broken-lines effect on the sides and the spots on the breast and snout remain apparent [1]---------- *Stephanolepis setifer.*

Genus *Amanses* Gray

A. A single species---------- *Amanses pullus.*

DESCRIPTION OF GENERA AND SPECIES

Monacanthidae is the correct name for this group of fishes, although the name Aluteridae was used by Fraser-Brunner (1941: p. 176) and others. Whitley (1929: p. 138) stated that "*Aluterus* Cloquet is an earlier name than *Monacanthus* Shinz, the first Latinization of 'Les Monacanthes' Cuvier, so the family hitherto known as Monacanthidae should be named Aluteridae." Two factors govern the propriety of family names—priority of the generic names as they have been used as family names, and, especially in the case of well-known groups, the generally used and accepted name that has become attached to a family (International Trust for Zoological Nomenclature, 1953: p. 33, art. 45(1)). Both of these factors apply to the acceptability of the name Monacanthidae. A review of the literature and abstracting journals clearly supports the more common acceptance of this name. In addition, Gill (1884: p. 417) gives "Monacanthini, Nardo . . . 1844" as the name used earliest and also gives five other uses of *Monacanthus* as a family group name that predate the first use of *Alutera* (in 1873) as a family group name (p. 416).

The separation of Monacanthidae (under the name of Aluteridae) as a family distinct from Balistidae by Fraser-Brunner (1941) provides adequate justification for this subjective distinction, although some recent authors have not acknowledged the separation and have treated Monacanthidae as a subfamily of Balistidae. In addition to the trenchant characters given by Fraser-Brunner, comparison of larval forms—larval Monacanthidae are very laterally compressed, contrasted with the laterally expanded and rotund larval Balistidae—provides additional reason for the familial separation. Fraser-Brunner's (1941: p. 176) separation follows:

> The division Balistiformes of the suborder Balistoidea consists of two families, which are separable as follows:
>
> I. Palatine T-shaped, the foot of the T movably articulated with the ectopterygoid. 8 outer teeth in each jaw; 6 inner ones in upper jaw. 2 or no caudal vertebrae with epipleurals. 5 precaudal interneurals; [2] 4 forming trough for spinous dorsal fin, the first movably articulated between exoccipitals, the others free from skull; the fifth forming a prop between trough and vertebral column. Distal ends of caudal interneurals and interhaemals not expanded. 3 dorsal spines. Scales moderate or small, in regular series, imbricate. All soft fins with branched rays---------- Balistidae.

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[1] The described pigmentations develop between 22 and 27 mm. S.L. We record specimens that have 30 soft rays in the dorsal or anal fins and lack the definitive pigment pattern as specifically unidentifiable.

[2] "Excepting one, which may be thickened, in series with the caudal interneurals, in front of soft dorsal fin" (Fraser-Brunner, 1941; p. 176).

II. Palatine a simple bar, not directly connected with ectopterygoid. 6 outer teeth in each jaw; 4 inner ones in upper jaw. 4 or 5 caudal vertebrae with epipleurals. 3 precaudal interneurals [2] fused to form trough for spinous dorsal fin, immovably attached to exoccipitals, unconnected with vertebral column. Distal ends of caudal interneurals with prominent lateral expansions. Normally 2 dorsal spines, the second very small and sometimes absent. Scales small or minute, not in regular series, rarely in contact. Soft dorsal, anal and pectoral rays simple--Aluteridae [Monacanthidae].

Alutera CLOQUET 1816

Aluterus as first proposed by Cloquet (1816: p. 135) is correctly emended to *Alutera* because the stem, *aluta*, is a feminine noun (Andrews, 1851: p. 89) and thus is in accord with the Copenhagen decisions on zoological nomenclature (International Trust for Zoological Nomenclature 1953: p. 49, art. 84(1)). Cloquet's proposal of the name appeared in a French dictionary and was based on a manuscript of Cuvier. Cuvier's (1817: p. 153) first application of the name, however, was in the vernacular, "Les Aluteres." Oken (1817: p. 1173) furnished *Alutera* in its nomenclatorially acceptable form. This genus includes the following nominal genera as synonyms: *Ceratacanthus* Gill 1861, *Osbeckia* Jordan and Evermann 1898, and *Davidia* Miranda Ribeiro 1915. Fraser-Brunner (1941: p. 187) separated the first two of these names as subgenera of *Alutera* on the basis of fin-ray counts and shape of the snout and caudal peduncle.

We recognize four species of *Alutera* from the western North Atlantic: *Alutera monoceros* (Linnaeus) 1758, *Alutera scripta* (Osbeck) 1765, *Alutera schoepfii* (Walbaum) 1792, and *Alutera heudelotii* Hollard 1855. A fifth species, *Alutera punctata* (Cuvier) *in* Spix 1831, has been reported from this area, but we regard it as a synonym of *Alutera schoepfii*, and it is discussed under the account of that species.

Alutera heudelotii, *A. scripta*, and *A. monoceros* possess an external, rudimentary pelvic spine near the distal end of the pelvic bone. This spine usually has several short, thick, and irregular barbs, that appear to wear off in large specimens. On some of the largest specimens the pelvic spine could not be located, presumably because of its degeneration and the corresponding increase in number and thickness of the spines on the body scales in this area. At its maximum development on smaller fish, the barbs of this rudimentary spine are much thicker and extend farther from the body surface than the spines of the associated body scales (fig. 5). This type of spine does not occur in *Alutera schoepfii*, and therefore its presence or absence is useful in distinguishing this species from *A. heudelotii*, particularly so in specimens 50 to 90 mm. S.L. where other characters used to separate these two species are relative or overlapping. This spine was found in all specimens of *Alutera heudelotii* from 30.5 to 135 mm. S.L., but could not be located in specimens of 136 mm. S.L. and larger. It was noted in specimens of *A. monoceros* from 53 to 137 mm. S.L. In *A. scripta*, it was noted in specimens from 27 to 200 mm. S.L. Smith (1935: p. 359, pl. XLII D) recorded pelvic spines in *A. monoceros* and *A. scripta* from South Africa.

Longley (1935: p. 86) noted the pelvic spine in *Alutera ventralis* and referred to it as "a microscopic vestige of the reduced ventral girdle of *Monacanthus*." Hildebrand (*in* Longley and Hildebrand, 1940: p. 279) corroborated its presence in this species, but described it as freely movable in the skin. The skin surrounding the spine can readily be lifted away from the bone, and we have found the spine to be directly fused to the pelvic bone. However, the spine can be broken away from the bone, and if retained in position in the surrounding skin it is then movable. We have not determined a homologous relationship between this rudimentary spine and the pelvic spine of *Monacanthus*, *Stephanolepis*, or *Amanses*, and accept Longley's interpretation only on circumstantial evidence.

Alutera monoceros (Linnaeus) 1758

(Figures 19, 20, and 21)

This species was described in a pre-Linnaean publication by Osbeck (1757) from a specimen taken off the coast of China. The name was documented nomenclatorially by Linnaeus in 1758. Some authors have regarded *Alutera monoceros* as a Pacific species and have distinguished the Atlantic form under the name of *Alutera guntheriana* Poey 1863; but comparisons of our Atlantic material with specimens from the China Sea and the Philippines show them to be identical in all respects, and we regard *Alutera monoceros* as a species of worldwide occurrence. Comparisons of specimens from the western North Atlantic with specimens from Brazil, South Africa, and the Pacific coast of Panama show slight differences in contour and depth, but we attribute this to individual variation and perhaps varying rates of ontogeny in different geographical areas.

Diagnostic characters.—Dorsal spines, 2. Dorsal soft rays, 46 to 50; anal soft rays, 47 to 52 (table 1). Pectoral spine, 1 rudimentary. Pectoral soft rays, 14 (table 11). Pelvic spine, rudimentary and not movable (as *Alutera heudelotii* in fig. 5), absent in large specimens. Gill slit, oblique at an angle of about 45° to horizontal to body axis (as in fig. 4). First dorsal spine, inserted over middle or posterior part of eye (as in fig. 4). No deep groove behind dorsal spines. Body depth, 34.4 to 43.8% S.L. (table 12; fig. 35). Head length, 26.6 to 34.7% S.L. (table 13). Snout length, 23.4 to 27.5% S.L. (table 14). Eye diameter, 4.2 to 8.3% S.L. (table 15). Eye to dorsal spine distance, 7.0 to 8.6% S.L. (table 16). Caudal peduncle longer than deep; peduncle length into peduncle depth 0.65 to 0.95 times. Caudal fin relatively short, about 18 to 26% S.L.

Specimens examined.—From the western North Atlantic: 10 of 53 to 545 mm. S.L., from southern Massachusetts, the Carolinas, eastern Florida, and the Florida Keys (fig. 38).

Alutera scripta (Osbeck) 1765

(Figures 9, 19, 20, and 22)

This species has usually been regarded as of worldwide distribution. We have examined specimens from Hawaii, Okinawa, and the Pacific coast of Panama that appear to be identical with our western Atlantic material. Whitley (1952: p. 30) attempted to limit the Atlantic population under the name of *Osbeckia picturata* (Poey) 1863.

The brief description of *Balistes scriptus* that has been assigned to this species was in a publication by Osbeck (1757: p. 111) that predates nomenclatorial acceptability. Linnaeus did not record this name in the tenth edition of his Systema Naturae, although he did include (1758: p. 327) the listing of Osbeck's *Balistes monoceros* from the preceding page of Osbeck's book (1757: p. 110). The first nomenclatorially acceptable publication of the name *scripta* is in a translation of Osbeck's 1757 book from Swedish to German by J. G. Georgi in 1765 (p. 145). Since Georgi apparently made a direct translation without any emendations, we do not consider him as the author of Osbeck's names and descriptions.

Diagnostic characters.—Dorsal spines, 2. Dorsal soft rays, 43 to 49; anal soft rays, 46 to 52 (table 2). Pectoral spine, 1 rudimentary. Pectoral soft rays, 13–15 (table 11). Pelvic spine, rudimentary and not movable (as *Alutera heudelotii* in fig. 5), absent in large specimens. Gill slit, oblique at an angle of about 45° to horizontal body axis on specimens larger than 40 mm. S. L. (as in fig. 4). First dorsal spine, inserted over middle or posterior part of eye (as in fig. 4). No deep groove behind dorsal spines. Body depth, 21.5 to 35.0% S. L. (table 12; fig. 35). Head length, 29.3 to 33.9% S. L. (table 13). Snout length, 21.9 to 28.8% S. L. (table 14). Eye diameter, 5.3 to 9.1% S. L. (table 15). Eye to dorsal spine distance, 5.0 to 6.7% S. L. (table 16). Caudal peduncle deeper than long on specimens larger than 30 mm. S. L.; peduncle length into peduncle depth 1.24 to 1.60 times on specimens larger than 50 mm. S. L., 1.03 to 1.05 times on specimens of 31 to 46 mm. S. L., 0.86 on a 27-mm. S. L. specimen. Caudal fin relatively long, about 33 to 61% S. L.

Specimens examined.—From the western North Atlantic: 48 of 27 to 377 mm. S. L. (skin and skull examined of a specimen about 410 mm. S. L.) from Bermuda, off the North Carolina coast, southward around Florida, in the Gulf of Mexico, and the Caribbean (fig. 38).

Color.—In live specimens taken off North Carolina in September 1959, the scrawled markings and spots were dark green and the background color was mottled olive-brown. This color fades and may disappear upon preservation, but the pigmentation in the markings and spots remains dark on most specimens even after prolonged preservation.

Alutera schoepfii (Walbaum) 1792

(Figures 10, 11, 23, and 24)

This species is extremely variable in certain morphological characters. Early in the study when we had only a few specimens, it appeared that two forms existed, one of which we would have called *Alutera punctata* (Cuvier) *in* Spix,

1831. Specimens were examined that were extremely diverse in eye diameter, distance from eye to dorsal spine, shape of the snout to dorsal spine profile, body depth, and pigmentation. However, when our complete size series of specimens had been acquired and examined, we found that the specimens intermediate in these morphological characters were more abundant than the extremely diverse specimens. We were convinced that these specimens represented a single highly variable species. If *A. punctata* exists, we have no specimens of it, and there is no available publication to differentiate it from *A. schoepfii*. The inadequacy of the original description of *A. punctata* was pointed out by Longley (*in* Longley and Hildebrand, 1941: p. 292). Longley also examined the specimen Jordan and Rutter (1897: p. 127) used for the first redescription of *A. punctata*, and considered it to be *A. schoepfii*. We assume artist's license in the excessively low numbers of dorsal fin rays and high numbers of body spots on the drawing of the type specimen of *A. punctata* (*in* Spix, 1831, pl. LXXVI). "Cuv. in litt." is given by Agassiz as the author of this species (*in* Spix, 1831: p. 137), inferring that Cuvier should be recorded as the author of this name.

Diagnostic characters.—Dorsal spines, 2. Dorsal soft rays, 32 to 39; anal soft rays, 35 to 41 (table 3). Pectoral spine, 1 rudimentary. Pectoral soft rays, 11 to 14 (table 11). Pelvic spine, absent at all sizes. Gill slit, oblique at an angle of about 45° to horizontal body axis on specimens larger than 40 mm. S.L. (as in fig. 4). First dorsal spine, inserted over mid or posterior part of eye (as in fig. 4). No deep groove behind the dorsal spines. Body depth, 17.3 to 47.4% S.L. (table 12; fig. 35). Head length, 23.3 to 34.2% S.L. (table 13). Snout length, 12.0 to 28.6% S.L. (table 14). Eye diameter, 4.8 to 8.8% S.L. (table 15). Eye to dorsal spine distance, 3.9 to 13.5% S.L. (table 16; fig. 34).

Specimens examined.—258 of 15.0 to 410 mm. S.L., from Bermuda, from Nova Scotia southward along the eastern and Gulf coasts of the United States, and from along the coasts of Cuba, Jamaica, Haiti, Atlantic Panama, and Brazil (fig. 38).

Color.—In live specimens taken off North Carolina in September 1959, the coloration was variable with background shades of white, orange, or metallic gray. When white was present, it was usually most prevalent over the anterior regions of the fish. Orange was nearly always present, at least in the form of spots along the midventral region of the body. The dark metallic gray color was often present on the dorsal half of the body as well as on the peduncle. In a few specimens the body was entirely dark, but even in these orange spots were present, and in several specimens the orange spots were extremely numerous. Usually when the anterior regions of the fish were white, some orange blotches extended onto the white background. Often the dark gray occurred as large blotches over the orange. The entire coloration fades rapidly when specimens are placed in a preservative—the orange spots are extremely ephemeral.

Alutera heudelotii **Hollard 1855**

(Figures 12 and 25)

Alutera heudelotii Hollard (1855: p. 13, described from Senegal, West Africa) occurs in both the eastern and western Atlantic, and its synonymy has only recently been determined.[3] It includes the following nominal species: *Alutera fuscus* (Fischer, 1885: p. 75, pl. II, fig. 6, from Cameroon, West Africa); *Alutera blankerti* (Metzelaar, 1919: p. 295, fig. 64, from Cape Blanco, West Africa); and *Alutera ventralis* (Longley, 1935: p. 68, from Tortugas, Florida; redescribed by Hildebrand in Longley and Hildebrand, 1940: p. 278).

This species has largely been overlooked or confused, and we have re-identified specimens in several museums that were incorrectly identified as *A. scripta*, which species it superficially resembles, and as *A. schoepfii* and its synonym *A. punctata*. A number of early and recent references to *A. punctata* were undoubtedly based on specimens of *A. heudelotii*. The 44-mm. specimen from off West Africa described and illustrated as *A. blankerti* by Poll (1959: p. 247, fig. 83) represents this species, as does the 291-mm. West African specimen Poll illustrated as *A. punctatus* (1959: fig. 82).

Diagnostic characters.—Dorsal spines, 2. Dorsal soft rays, 36 to 41; anal soft rays, 39 to 44 (table 4). Pectoral spine, 1 rudimentary. Pectoral soft rays, 12 to 14 (table 11). Pelvic spine, rudimentary and not movable (fig. 5), absent in specimens larger than 135 mm. S.L. Gill slit, oblique at an angle of about 45° to horizontal body axis in specimens larger than 40 mm. S.L. (fig. 4). First dorsal spine, inserted over mid or posterior part of eye (fig. 4). No deep groove behind dorsal spines. Body depth, 27.6 to 46.5% S.L. (table 12; fig. 35). Head length, 29.1 to 35.2% S.L. (table 13). Snout length, 23.8 to 28.7% S.L. (table 14). Eye diameter, 6.2 to 10.0% S.L. (table 15). Eye to dorsal spine distance, 4.0 to 7.3% S.L. (table 16; fig. 34).

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[3] Berry, Frederick H., and Max Poll. Manuscript, Synonymy of the Atlantic Ocean filefish *Alutera heudelotii* Hollard.

Specimens examined.—68 of 30.5 to 240 mm. S.L., from Bermuda, from southern Massachusetts, off the coast of the Carolinas, around the Florida coast, in the Gulf of Mexico, and off Brazil (fig. 38).

Color.—In live specimens taken off North Carolina in September 1959, the scrawled markings and spots were bluish purple; the background color was a mottled olive brown that faded upon preservation. The pigmentation of the markings and spots remains dark on most specimens even after prolonged preservation.

Monacanthus OKEN 1817

We have examined two valid species of this genus from the western North Atlantic, *M. tuckeri* Bean 1906 and *M. ciliatus* (Mitchill) 1818.

The two species of *Monacanthus* in the western North Atlantic were recorded in a new subgenus, *Leprogaster*, by Fraser-Brunner (1941: p. 184). He distinguished it as an Atlantic subgenus characterized by a shorter pelvic spine and a smaller ventral flap than are present in the Pacific subgenus *Monacanthus*. We found no elongation of the upper caudal ray in the Atlantic species as was depicted by Fraser-Brunner for his new Pacific species, *Monacanthus macrolepis* (1941: p. 190, fig. 4).

Monacanthus tuckeri apparently is a smaller species than *M. ciliatus*, both in not growing to so large a size and in maturing at a smaller size. Based on the specimens we examined it appears to be the less abundant of the two along the United States coast, but more equally common with *M. ciliatus* in the Bahamas and Bermuda.

In his revision of the Aluteridae Fraser-Brunner (1941) recorded both *Monacanthus* and *Stephanolepis* as valid and distinct genera. Since then several workers have disagreed with this pronouncement and have regarded *Stephanolepis* as a synonym of *Monacanthus*. The probable reason for this disagreement is the interpretation of scale structure of the two nominal genera. We have found the scale structure is subject to ontogenetic change—not adequately accounted for by Fraser-Brunner. Scales of various sizes of specimens of *Stephanolepis hispidus* and *Monacanthus ciliatus* are diagrammatically illustrated in figure 8. In the structure and ontogeny of its scales, *Stephanolepis setifer* is essentially similar to *S. hispidus*, as is *Monacanthus tuckeri* to *M. ciliatus*, except that *M. tuckeri* is smaller at maturity than is *M. ciliatus* and exhibits changes in its scale structure at smaller sizes.

The scales of all four genera of filefish examined during this study have one or more spines arising perpendicularly from the scale base, the number of spines increasing with growth or size of the fish. Above the scale base the spines are usually curved posteriad, and they may undergo certain modifications as secondary sexual characteristics, particularly in the region of the caudal peduncle. The scales of *Alutera* and *Amanses* are similar to those of *Monacanthus*. The scales of *Monacanthus* and *Stephanolepis* are similar up to a size of about 20 mm. S.L., the scales of each having a single spine (fig. 8). At sizes larger than 20 mm. S.L., the spines of some of the scales of *Stephanolepis* have become branched—this branching occurs well above the scale base usually on the distal one-fourth of the spine. Between 30 and 40 mm. S.L. the spines of essentially all of the scales of *Stephanolepis* have become branched. Two or more closely joined spines are present on scales of *Stephanolepis* of more than 100 mm. S.L., and eight were present on the scales of a 150-mm. S.L. specimen—all of these spines are branched. Conversely, the scale spines of *Monacanthus* never branch—each spine arises individually from the scale base. Two spines were found on a few scales of a 41-mm. S.L. specimen of *Monacanthus ciliatus*, three at 46.5 mm. S.L., and seven at 95 mm. S.L. (fig. 8). Some of the spines on larger specimens of *Monacanthus* are joined basally by a thin bony partition.

After analyzing these concrete differences in scale structure in the two groups, as well as distinct differences in secondary sexual characters, we recognize the value of Fraser-Brunner's generic distinction of *Stephanolepis* from *Monacanthus*.

The pelvic spine in *Monacanthus* is very similar to that in *Stephanolepis* (fig. 5).

Monacanthus tuckeri Bean 1906

(Figures 13 and 29)

Although this species was described more than 50 years ago, it has never been adequately distinguished from *Monacanthus ciliatus*, and many museum collections we have examined contained both species, usually cataloged as *M. ciliatus*.

Diagnostic characters.—Dorsal spines, 2. Dorsal soft rays, 32 to 37; anal soft rays, 31 to 36 (table 5). Pectoral spine, 1 rudimentary. Pectoral soft rays, 10 to 12 (table 11). Pelvic spine, large and movable (as in *Stephanolepis;* fig. 5). Gill slit, nearly vertical with respect to horizontal body axis (as in *Stephanolepis;* fig. 4). First dorsal spine, inserted over posterior part of eye (as in *Stephanolepis;* fig. 4). No deep groove behind dorsal spines. Body depth, 31.3 to 38.6 % S.L. (table 12; fig. 36). Head length, 33.1 to 41.5 % S.L. (table 13). Snout length, 20.7 to 28.2 % S.L. (table 14). Eye diameter, 8.7 to 14.4 % S.L. (table 15). Eye to dorsal spine distance, 6.3 to 10.6 mm. S.L. (table 16).

Specimens examined.—60 of 15.3 to 56.5 mm. S.L., from Bermuda, off the Carolinas, off eastern Florida, in the Bahamas and the Lesser Antilles (fig. 39).

Sexual characters.—The seven largest specimens available had gonads large enough to permit determination of sex (2 males, 56.5 and 50.5 mm. S.L.; 5 females, 53, 51.5, 50.5, 49, and 48 mm. S.L.). The next largest specimens, 44 and 36 mm. S.L., had visible gonads, but they were too small for the sex to be interpreted. The males have a dorsal and a ventral pair of enlarged recurved spines on each side of the caudal peduncle, and the spines on other scales on the sides of the peduncle are elongated, forming a bristlelike patch. The females have similar pairs of spines on the peduncle but they are smaller and are directed posteriorly, and the spines of scales on the peduncle are not much, if any, larger than other body scale spines. These dorsal and ventral pairs of spines are discernible on specimens as small as 19 mm. S.L., since at this size and larger the scale bases from which they arise are larger (of greater diameter) than the bases of the other peduncle scales. The larger or more expandible ventral flap of the male with the dark stripe near its margin was described and illustrated by Clark (1950: p. 162). Clark listed males of 39, 59, and 60 mm. S.L., a female of 45 mm. S.L., and immature specimens of 17 to 30 mm. S.L.

Monacanthus ciliatus (Mitchill) 1818

(Figures 14, 15, 29, and 30)

As noted before, this species has frequently been confused with *Monacanthus tuckeri*.

Diagnostic characters.—Dorsal spines, 2. Dorsal soft rays, 29 to 37; anal soft rays, 28 to 36 (table 6). Pectoral spine, 1 rudimentary. Pectoral soft rays, 9 to 13 (table 11). Pelvic spine, large and movable (as in *Stephanolepis;* fig. 5). Gill slit, nearly vertical with respect to horizontal body axis (as *Stephanolepis;* fig. 4). First dorsal spine, inserted over posterior part of eye (as in *Stephanolepis;* fig. 4). No deep groove behind dorsal spines. Body depth, 39.1 to 54.5 % S.L. (table 12; fig. 36). Head length, 29.0 to 38.7 % S.L. (table 13). Snout length, 16.4 to 25.7 % S.L. (table 14). Eye diameter, 7.4 to 14.5 % S.L. (table 15). Eye to dorsal spine distance, 6.7 to 10.1 % S.L. (table 16).

Specimens examined.—347 of 11.0 to 111 mm. S.L., from Bermuda, Massachusetts, the coast of the Carolinas, around Florida, in the Gulf of Mexico, the Bahamas, and throughout the Caribbean (fig. 39).

Sexual characters.—Clark (1950: p. 159) described the sexual characters of this species. Immature specimens have a dorsal and a ventral pair of posteriorly directed spines on each side of the caudal peduncle—discernible on specimens as small as 20 mm. S.L. In the three largest females we examined (92.5, 101, and 109 mm. S.L.) the anterior spine of each pair was slightly recurved. In male fish larger than about 60 mm. S.L., these spines enlarge and become strongly recurved. Although the original pairs of spines remain distinct, additional and similar spines form with growth—the largest male examined (107 mm. S.L.) had 5 dorsal and 4 ventral spines on each side. On males 90 mm. S.L. and larger, the spines on the other scales on the sides of the peduncle are elongated, forming a bristlelike patch.

Stephanolepis GILL 1861

After examination of thousands of specimens of this genus from the western North Atlantic, we were able to distinguish only two species—*S. hispidus* (Linnaeus) and *S. setifer* (Bennett). The name *setifer* was applied to specimens from Cuba and Atlantic Colombia with a relatively low number of fin rays (D. 27–28, A. 26–27) by Fraser-Brunner (1940: p. 519). His reasons for applying and restricting this name certainly appear to be justified. *Stephanolepis setifer* is identical with *Monacanthus oppositus* Poey described by Meek and Hildebrand (1928: p. 798) from Panama, but we can not confirm their species range of from Massachusetts to Brazil.

Five species of *Stephanolepis* were identified from the western Atlantic by Fraser-Brunner (1940). *S. setifer* has low numbers of fin rays, whereas the other four species were reported to have 30 or more dorsal and anal rays. *S. insignis* Fraser-Brunner 1940 and *S. varius* (Ranzani) 1842 were recorded from Brazil. Our specimens of *Stephanolepis* do not represent either of these forms; their distinguishing characteristics are not too convincing; none has been recorded from the western Atlantic with the exception of the type material. The remaining two species reported by Fraser-Brunner were *S. hispidus* (Linnaeus) 1758 and *S. spilonotus* (Cope) 1871. We record *S. spilonotus* as a synonym of *S. hispidus*, because we judge our specimens to represent a single species with moderate variation in morphological characters, and because we found a complete overlap in every character that Fraser-Brunner (1940: p. 523, 535) used to separate the two nominal species. Certainly there is no difference between populations of *S. hispidus* from the Atlantic and from the Gulf of Mexico, as his observations suggest. The five specimens Fraser-Brunner designated as *S. spilonotus* from Florida, Mississippi, and Cuba in the Museum of Comparative Zoology cannot be located.

In *Stephanolepis* the first dorsal spine has two rows of large, ventrally directed barbs on its posterior margin. The number of barbs present is difficult to count, because those near the base of the spine abruptly decrease in size, particularly in larger specimens; but the number of these barbs has been used previously as a taxonomic character (Fraser-Brunner, 1940: p. 523) to separate *S. hispidus* with 6 or 7 strong barbs from *S. spilonotus* with 12 or more small barbs. We have determined two features that invalidate this character: (1) the barbs become relatively smaller as the fish increases in size, and (2) the number of barbs increases with growth of the fish. The following counts of barbs from one side of the spine of *S. hispidus* illustrate this second invalidating feature (standard length in millimeters and number of barbs in parentheses): 8.4 (3), 8.9 (2), 9.5 (3), 16 (3), 16.5 (3), 16.5 (2), 17 (3), 17.5 (2), 18 (2), 20 (3), 24.5 (4), 26.5 (4), 29.5 (2), 42.5 (5), 44 (5), 48 (5), 52.5 (6), 59 (6), 62 (5), 66 (5), 67 (6), 70 (6), 72 (6), 72 (7), 73 (8), 81 (10), 83 (8), 97 (8), 114 (8), 122 (10), 136 (8), 139 (11), 142 (10), 143 (12), 145 (9), 151 (11), 158 (13), 167 (11). Frequently the number of barbs on each side of the back of the spines varies by 1 or 2, and in these cases the count from the side having the greater number of barbs was recorded.

It is characteristic that a small percentage of specimens of most of the species of Monacanthidae examined had a background pigmentation much darker than average. This was observed in specimens preserved in both alcohol and formalin. Conversely, some few of the preserved specimens were almost unpigmented. This caused some difficulty in confirming pigmentation characteristics for *S. hispidus* and *S. setifer*, but usually when moist specimens were examined the correct determination could be made (drying or partly drying of specimens makes the pigmentation more difficult to see). This feature produces excessive difficulties in utilizing the key to the species of *Stephanolepis* by Fraser-Brunner (1940: p. 521), in which the primary couplet concerns pigment (longitudinal pattern of bars, patches, or bands *vs.* transverse and mottled pattern).

The profile from snout to dorsal spine of *S. hispidus* is concave in most specimens, but in some it is nearly straight, and in others slightly convex.

The distance from the upper edge of the orbit to the base of the first dorsal spine in *S. hispidus* is also variable and may be either greater or less than the diameter of the eye.

We have found no specimens of *Stephanolepis setifer* from the coast of the United States, where *S. hispidus* is relatively common. Analysis of the specimens examined indicates that *S. setifer* is more common around Cuba, Jamaica, other islands of the West Indies, and in open waters of the Gulf Stream or Florida Current. Apparently it is a smaller species than *S. hispidus*, maturing at a smaller body size.

The relationship of this genus to *Monacanthus* is discussed under the generic account of *Monacanthus*. Photomicrographs of the scale structures of *Stephanolepis* (under the name of *Stefanolepis hispidus*) were published by Sanzo (1930, pl. III, figs. 32–35).

The pelvic spine of *Stephanolepis hispidus* and of *S. setifer* possesses barbs and is articulated with the end of the barbed portion of the pelvic bone that protrudes through the skin (fig. 5). It is freely movable for a short distance (about 45°) in an anteroposterior direction.

The color patterns on sides, breast, and caudal fin are of about equal value in separating the two species; that is, the prominence of one of the characters is usually accompanied by an equal prominence of the other two. At sizes less than about 22 mm. S.L. the species cannot be separated on this basis as the patterns described below are nearly always absent. From about 22 mm. to about 27 mm. these patterns are often present. Specimens between about 27 to 65 mm. normally have good and distinguishable color patterns; the pattern tends to become less distinguishing at the larger sizes. **Sides:** *S. setifer* normally has more rows of dashes arranged longitudinally, giving a broken-lines effect, the dashes being narrower and more sharply defined than the corresponding small bars and spots of *S. hispidus;* and both species have similar broad, dusky bands of varying intensity, that may be vertical or oblique. **Breast:** Both species have the broad dusky bands continuing onto the breasts, but in addition, *S. setifer* has few to many small flecks or spots, especially in the region ventral to and anterior to the bases of the pectoral fins; these flecks are entirely absent in *S. hispidus*. **Caudal fin:** Both species have two dark vertical bands on the caudal fin, however, these bands are narrower and usually much darker in *S. setifer;* the first band in *S. setifer* is usually much darker than the second, while in *S. hispidus* both bands are of about equal intensity and not very prominent.

Stephanolepis hispidus (Linnaeus) 1758

(Figures 16, 17, 31, 32, and 33)

The close relationship of this species to *Stephanolepis setifer* has been discussed under the account of the genus.

Diagnostic characters.—Dorsal spines, 2. Dorsal soft rays, 29 to 35; anal soft rays, 30 to 35 (tables 7 and 10). Pectoral spine, 1; rudimentary at larger sizes, pronounced in larvae (see fig. 16). Pectoral soft rays, 12 to 14 (table 11). Pelvic spine, large and movable (fig. 5). Gill slit, nearly vertical with respect to horizontal body axis (fig. 4). First dorsal spine, inserted over posterior part of eye (fig. 4). No deep groove behind dorsal spines. Body depth, 43.3 to 65.8% S.L. (table 12; fig. 37). Head length, 29.5 to 41.4% S.L. (table 13). Snout length, 14.4 to 27.5% S.L. (table 14). Eye diameter, 6.9 to 17.1% S.L. (table 15). Eye to dorsal spine distance, 7.3 to 17.1% S.L. (table 16).

Specimens examined.—3,539 of 5.6 to 211 mm. S.L., from Georges Bank southward all along the Atlantic and Gulf coasts of the United States, off Mexico and Brazil (fig. 40).

It has been suggested (Fraser-Brunner, 1940: p. 535) that the number of dorsal and anal fin rays is greater in specimens from more northern localities than from more southern localities. The following values tend to indicate such a trend: Eighty-seven specimens from the Gulf of Mexico ranged from D 29–A 30 to D 34–A 34 with a 26.2-percent mode at D 32–A 32; 267 specimens from Georgia ranged from D 30–A 31 to D 34–A 33 with a 27.3-percent mode at D 32–A 32; 199 specimens from North Carolina ranged from D 31–A 31 to D 35–A 35 with a 29.6-percent mode at D 33–A 33: but a smaller sample of 20 specimens from Massachusetts ranged from D 32–A 32 to D 34–A 34 with a 40-percent mode of D 33–A 32, intermediate between that of Georgia and North Carolina.

Sexual characters.—Two secondary sexual characters develop on maturing males: the second soft ray of the dorsal fin becomes very elongated, and the spines of the scales on the sides of the caudal peduncle become prolonged and form a patch of bristles. The elongation of the second dorsal soft ray begins between about 104 and 128 mm. S.L. The patch of bristles on the peduncle forms between about 104 and 134 mm. On specimens larger than 140 mm. the elongated second soft ray of the dorsal fin was 21 to 95 mm. longer than the third soft ray. No secondary sexual characters were found in females. Although females average a slightly greater body depth than males, appreciable variation occurs in this character and the values for the sexes overlap.

The following observations were made on a sample of 140 specimens of 73.5 to 211 mm. S.L. taken by bottom trawling on the M/V *Silver Bay* off the coast of North Carolina during September 1959:

Seven immature specimens or specimens with gonads too small to be evaluated, 73.5 to 95 mm. (mean, 85.3 mm.); 62 males, 78 to 211 mm. (mean, 131.8 mm.); 71 females, 77 to 180 mm. (mean, 120.1 mm.) of which five (146 to 180 mm.) had large macroscopic eggs in the ovaries. Such large eggs were found in other specimens ranging from 81 to 139 mm. S.L., taken at other times and areas.

Occurrence.—The locations of specimens of *Stephanolepis hispidus* and *S. setifer* taken at the surface off the southeastern Atlantic coast of the United States on cruises of the *Gill*, *Combat*, and *Silver Bay* are shown in figure 41. These specimens were less than 70 mm. S.L., and represent developing young, the majority of which were being carried northward by the Gulf Stream. The total number of records and of specimens of *S. hispidus* was much greater than for *S. setifer*. The records of *S. hispidus* are distributed from inshore out to beyond the axis of the Gulf Stream, whereas the records of *S. setifer* are generally confined to the boundaries of the Stream.

On cruise 18 of the M/V *Silver Bay* off the North Carolina coast in September 1959, records were made of all of the bottom-trawling stations at which *Stephanolepis hispidus* was taken. Figure 42 shows that the species was broadly distributed over the area at that time. Most of these specimens were mature, and some of the females had macroscopic eggs and apparently were near spawning condition.

***Stephanolepis setifer* (Bennett) 1830**

(Figures 31 and 32)

The resemblance of this species to *Stephanolepis hispidus* has been discussed under the account of the genus.

Diagnostic characters.—Dorsal spines, 2. Dorsal soft rays, 27 to 30; anal soft rays, 26 to 30 (tables 8 and 10). Pectoral spine, 1 rudimentary. Pectoral soft rays, 11 to 13 (table 11). Pelvic spine, large and movable (fig. 5). Gill slit, nearly vertical with respect to horizontal body axis (fig. 4). First dorsal spine, inserted over posterior part of eye (fig. 4). No deep groove behind dorsal spines. Body depth, 46.8 to 59.6 % S.L. (table 12; fig. 37). Head length, 31.3 to 40.2 % S.L. (table 13). Snout length, 18.4 to 26.8 % S.L. (table 14). Eye diameter, 7.6 to 15.9 % S.L. (table 15). Eye to dorsal spine distance, 7.7 to 13.3 % S.L. (table 16).

Specimens examined.—139 of 11.0 to 136 mm. S.L., from Bermuda, the Carolinas, southward around Florida, into the Gulf of Mexico, and throughout the Caribbean (fig. 40).

Sexual characters.—Sex was determined on 37 specimens, 15 males of 56.5 to 136 mm. S.L., and 22 females of 46.5 to 98 mm. S.L.; 18 other specimens of 36 to 53.5 mm. S.L. were either immature or had gonads too small to be interpreted. Secondary sexual characters apparently are similar to those of *Stephanolepis hispidus*, except that *S. setifer* matures and secondary sexual characters develop at smaller sizes. The females showed no secondary sexual development. Females 62.5 to 98 mm. S.L. had large macroscopic ovarian eggs, but females of 76.5 mm. and of 61.5 mm. S.L. and smaller had microscopic eggs. Males 82.5 mm. S.L. and larger had a patch of bristles on each side of the caudal peduncle; smaller specimens lacked this bristle patch. All males examined had the second soft ray of the dorsal fin elongated: 5.5 mm. longer than the other rays in the 56.5-mm. S.L. male and more than 33 mm. longer in the 136-mm. S.L. male. A 98.5-mm male had the third ray elongated also, about one-half the extent of elongation of the second ray.

Amanses Gray 1833

Fraser-Brunner (1941) reduced *Cantherines* Swainson 1839 to subgeneric rank within the genus *Amanses* Gray 1833. The subgenus *Amanses* reportedly possesses "A patch of long spines on side between soft dorsal and anal fin, at least in male." Since this feature has never been reported for western North Atlantic monacanthids, *A. pullus* should be of the subgenus *Cantherines*.

The pelvic spine of *Amanses pullus* is fused to the end of the barbed portion of the pelvic bone that protrudes through the skin (fig. 5). It is similar to the pelvic spine of *Monacanthus* and *Stephanolepis*, but unlike the spine in those genera, it is not movable, unless damaged. (With excessive pressure the plane of fusion may part, and the spine may be abnormally movable.)

Amanses pullus (Ranzani) 1842

(Figures 18, 26, 27, and 28)

Ranzani (1842) described *Monacanthus pullus* from a large, blackish specimen without spines on the caudal peduncle, from the coast of Brazil. Cope (1871) described *Monacanthus amphioxys* from a smaller, lightly colored specimen, also without caudal spines, from St. Martins Island in the West Indies. The relationship of these two nominal forms is still uncertain, but we believe the forms are identical. The variation in color pattern of specimens 38 to 148 mm. S.L. was described by Clark (1950: p. 163) under the name of *Cantherines pullus*. In addition to her observations, we have examined a large freshly preserved female (158 mm. S.L., University of Florida 7266) that has a black body and caudal fin and the other fins pale or colorless. Larger specimens preserved for a long time have brownish bodies and clear fins.

Diagnostic characters.—Dorsal spines, 2. Dorsal soft rays, 33 to 37; anal soft rays 29 to 32 (table 9). Pectoral spine, 1 rudimentary. Pectoral soft rays, 12 to 14 (table 11). Pelvic spine, large and not movable, fused to pelvic bone (fig. 5). Gill slit, nearly vertical with respect to horizontal body axis (fig. 4). First dorsal spine, inserted over anterior part of eye on specimens 30 mm. S.L. and larger (fig. 4). A deep groove present behind the dorsal spines into which they can be depressed (fig. 27, B). Body depth, 38.6 to 49.3 % S.L. (table 12; fig. 37). Head length, 29.0 to 42.9 % S.L. (table 13). Snout length, 25.6 to 33.3 % S.L. (table 14). Eye diameter, 5.2 to 14.9 % S.L. (table 15). Eye to dorsal spine distance, 5.9 to 9.0 % S.L. (table 16).

Specimens examined.—99 of 17.5 to 325 mm. S.L., from Massachusetts, southward along the Atlantic coast, around the coast of Florida into the Gulf of Mexico, the Bahamas, and throughout the West Indies (fig. 39).

The specialized scalation and spination on the caudal peduncle (usually a sex-associated character) is not clearly understood. Two large fresh specimens with orange-colored curved spines on the peduncle have been reported to us (personal communications, Eugenie Clark, Cape Haze Marine Laboratory, and Craig Phillips, U.S. Fish and Wildlife Service). The three largest specimens examined have recurved spines on the peduncle—a 325-mm. S.L. male has 3 dorsal and 2 ventral strongly recurved spines on each side of the peduncle; a 322-mm. male has 2 dorsal and 2 ventral spines similarly located (both of these specimens have a patch of bristles extending from the recurved spines onto the body); a 288-mm. female has 2 dorsal and 2 anal spines on each side of the peduncle, that are smaller and only slightly recurved in comparison to the spines of the males, and the patch of bristles on the peduncle of this female is relatively smaller. A 182-mm. specimen (sex unknown) has 2 pairs of large recurved spines and sparse patches of bristles on each side of the peduncle. A 115-mm. specimen (sex unknown) has 2 pairs of small and only slightly recurved spines on each side of the peduncle. No other specimens of this species examined had paired peduncle spines. Specimens with patches of bristles on each side of the peduncle included females 136 and 158 mm. S.L., males 124 and 136 mm. S.L., and sex unknown 105, 123, 127, 131, and 138 mm. S.L. Several specimens between 100 and 142 mm. lacked these bristle patches, and no specimens less than 100 mm. had them. A 288-mm. female had large ovaries but no macroscopic eggs, although females of 158, 142, 136, and 136 mm. had large macroscopic eggs.

LITERATURE CITED

Anderson, William W., Jack W. Gehringer, and Edward Cohen.

1956. Physical oceanographic, biological, and chemical data, south Atlantic coast of the United States, M/V *Theodore N. Gill* Cruise 1. U.S. Fish and Wildlife Service, Special Scientific Report—Fisheries No. 178, 160 p., 15 figs.

Andrews, Ethan A.

1851. A copious and critical Latin-English lexicon . . . Harper & Bros., New York, 1663 p.

Bean, Tarleton H.

1906. Descriptions of new Bermudian fishes. Biological Society of Washington, Proceedings, vol. 19, p. 29–33.

Bennett, Edward Turner.

1830. Observations on a collection of fishes, formed during the voyage of H.M.S. "Chanticleer," with the characters of two new species. Zoological Society of London, Proceedings, vol. 1, p. 112.

Clark, Eugenie.

1950. Notes on the behavior and morphology of some West Indian plectognath fishes. Zoologica, vol. 35, no. 13, p. 159–168, figs. 1–7, pls. 1–2.

Cloquet, Hippolyte.

1816. Dictionnaire des Sciences Naturelles. Vol. 1, supplement, p. 135. F. G. Levrault, Strasbourg.

Cope, Edward D.

1871. Contribution to the ichthyology of the Lesser Antilles. American Philosophical Society, Transactions, vol. 14, p. 445–483.

Cuvier, Georges.

1817. Le Régne Animal . . . . Vol. 2, Deterville, Paris, 528 p.

Fischer, Johann Gustav.

1885. Ichthyologische und herpetologische Bemerkungan. II. Über einige afrikanische Fische des Naturhistorischen Museums in Hamburg. Jahrbuch der Hamburgischen. Wissenschaftlichen Anstalten, vol. 2, p. 66–77, pl. II.

Fraser-Brunner, Anton.

1940. Notes on the plectognath fishes. III. On *Monacanthus setifer* Bennett and related species, with a key to the genus *Stephanolepis* and descriptions of four new species. Annals and Magazine of Natural History, ser. 11, vol. 5, no. 30 (art. 51), p. 518–535, figs. 1–7.

1941. Notes on the plectognath fishes. VI. A synopsis of the genera of the family *Aluteridae*, and descriptions of seven new species. Annals and Magazine of Natural History, ser. 11, vol. 8, no. 45 (art. 16), p. 176–199, figs. 1–9.

Gill, Theodore Nichols.

1861. [Communication on several new generic types of fishes.] Academy of Natural Sciences of Philadelphia, Proceedings, vol. 13, p. 77–78.

1884. Synopsis of the plectognath fishes. U.S. National Museum, Proceedings, vol. 7, no. 448, p. 411–428.

Gray, John Edward.

1833. Illustrations of Indian zoology of new and hitherto unfigured Indian animals from the collection of General Hardwicke. Vol. 2. London.

Hollard H.

1855. Monographie de la Famille des Balistides. Annales des Sciences Naturelles, Zoologique, ser. 4, vol. 4, p. 5–27, pl. 1.

International Trust for Zoological Nomenclature.

1953. Copenhagen decisions on zoological nomenclature. 14th International Congress of Zoology. London. 135 p.

Jordan, David Starr, and Barton Warren Evermann.

1898. The fishes of North and Middle America: A descriptive catalogue of the species of fish-like vertebrates found in the waters of North America, north of Isthmus of Panama. U.S. National Museum, Bulletin No. 47 (pt. 3), p. 2183a–3136.

Jordan, David Starr, and Cloudsley Rutter.

1897. A collection of fishes made by Joseph Seed Roberts in Kingston, Jamaica. Academy of Natural Sciences of Philadelphia, Proceedings (3d. series), p. 91–133.

Linnaeus, Carl.

1758. Systema Naturae. . . . Laurentii Salvii, Holmiae. Ed. 10, vol. 1, 823 p.

Longley, William H.

1935. Osteological notes and descriptions of new species of fishes. Carnegie Institution of Washington, Yearbook, vol. 34, p. 86–89.

Longley, William H., and Samuel F. Hildebrand.

1940. New genera and species of fishes. Carnegie Institution of Washington, Publication No. 517 (Papers of the Tortugas Laboratory, vol. 32), p. 223–285, 28 figs., pl. 1.

1941. Systematic catalogue of the fishes of Tortugas, Florida, with observations on color, habits, and local distribution. Carnegie Institution of Washingtion, Publication 535 (Papers of the Tortugas Laboratory, vol. 34), 331 p., 34 pls. [Edited and completed by Samuel F. Hildebrand.]

Meek, Seth E., and Samuel F. Hildebrand.

1928. The marine fishes of Panama. Field Museum of Natural History Publication No. 249, Zoological Series, vol. 15, pt. 3, p. 709–1045, pls. 72–102.

Metzelaar, Jan.

1919. Report on the fishes, collected by Dr. J. Boeke, in the Dutch West Indies, 1904–1905, with comparative notes on marine fishes of tropical West Africa. *In* Boeke, J. (ed.); Rapport . . . in de Kolonie Curacao [etc.]. Firma F. J. Belinfanti, The Hague. 315 p., 64 figs.

Miranda Ribeiro, Alpio de.

1915. Fauna Brasiliense. Peixes. V. [Eleutherobranchios Aspirophores] Physoclisti. Archivo do Museu Nacional do Rio dé Janeiro, vol. 17, 777 p.

Mitchill, Samuel Latham.

1818. The fishes of New-York described and arranged. In a supplement to the Memoir on the same subject, printed in the New-York Literary and Philosophical Transactions, vol. 1, p. 355–492. American Monthly Magazine and Critical Review, February, vol. 2, no. 4, p. 242–248, 1 fig.; March, vol. 2, no. 5, p. 321–328.

Oken, L.

1817. Isis, p. 1182–1183 (misprinted 1782–1783). London. [Not seen.]

Osbeck, Pehr.

1757. Dagbok öfver en Ostindisk resa aren 1750–52, med anmärkningar uti naturkundigheten, frömmande folkslags sprak, ets. (En Ostindisk resa til Suratte, China, etc. Fran 1750 . . .). Ludv. Grefing, Stockholm, 376 p., 13 pls.

1765. Herrn Peter Osbeck. . . . Reise nach Ostindien und China. . . . Aus dem Schwedischen übersetzt von J. G. Georgi. J. C. Koppe, Rostock, 552 (28) p., 13 pls.

Poey, Felipe.

1863. Descriptions des poissons nouvelles ou peu connues. Academy of Natural Sciences of Philadelphia, Proceedings, vol. 15, p. 180–188. [*In* Ichthyological Papers, American Authors, vol. 8.]

Poll, Max.

1959. Poissons. IV. Teleosteens Acanthopterygiens (deuxieme partie). Expedition Oceanographique Belge dans les Eau Côtieres Africaines de l'Atlantique Sud (1948–1949), vol. 4, no. 3B, 417 p., 127 figs.

Ranzani, C.

1842. De novis speciebus piscium. Dissertatio secunda. Novi Comment. Acad. Sci. Inst., Bonon., vol. 5, p. 1–21, pls. 1–7.

Sanzo, Luigi.

1930. Ricerche biologiche su materiali raccolti dal Prof. L. Sanzo nella Campagna idrografica nel Mar Rosso della R. N. Ammiraglio Magnaghi 1923–1924. (VII). "Plectognati." R. Comitato Talassografico Italiano, Memoria 167, 111 p., pls. 1–7. Venezia.

Smith, James L. B.

1935. The South African species of the family Aluteridae. Albany Museum, Records, vol. 4 (pt. 2), p. 358–364, pls. 40–42.

Spix, Johann Baptist von.

1831. Selecta genera et species piscium quos in itinere per Brasiliam . . . . p. 83–138, pls. 49–101. C. Wolf, Monachii.

Swainson, William.

1839. The natural history and classification of fishes, amphibians, and reptiles, or monocardian animals. Vol. 2. London.

Walbaum, Johann Julius.

1792. Petri Artedi Sueci Genera piscium . . . . Emendata et aucta a Johanne Julio Walbaum. Grypeswaldiae, Ant. Ferdin. Rose, pt. 3, 723 p., 3 pls.

Whitley, Gilbert P.

1929. Studies in ichthyology. No. 3. Australian Museum, Records, vol. 17, no. 3, p. 101–143, figs. 1–5, pls. 30–34.

1952. Figures of some Australian fish types. Royal Zoological Society of New South Wales, Proceedings, 1951–1952, p. 23–31, figs. 1–8.

APPENDIX

FIGURES

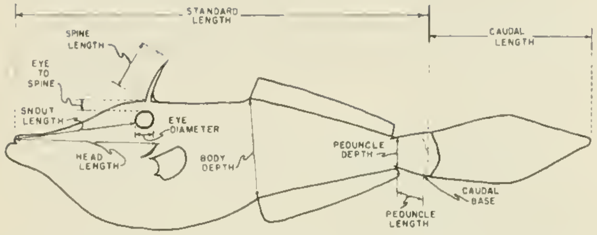

FIGURE 1.—Diagram of a filefish showing measurements used in this study.

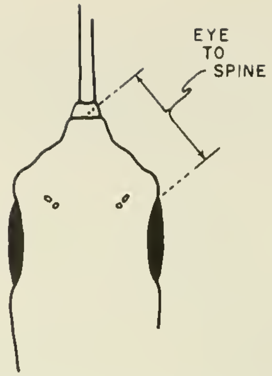

FIGURE 2.—Enlarged front view of upper part of head showing measurement from eye to insertion of dorsal spine.

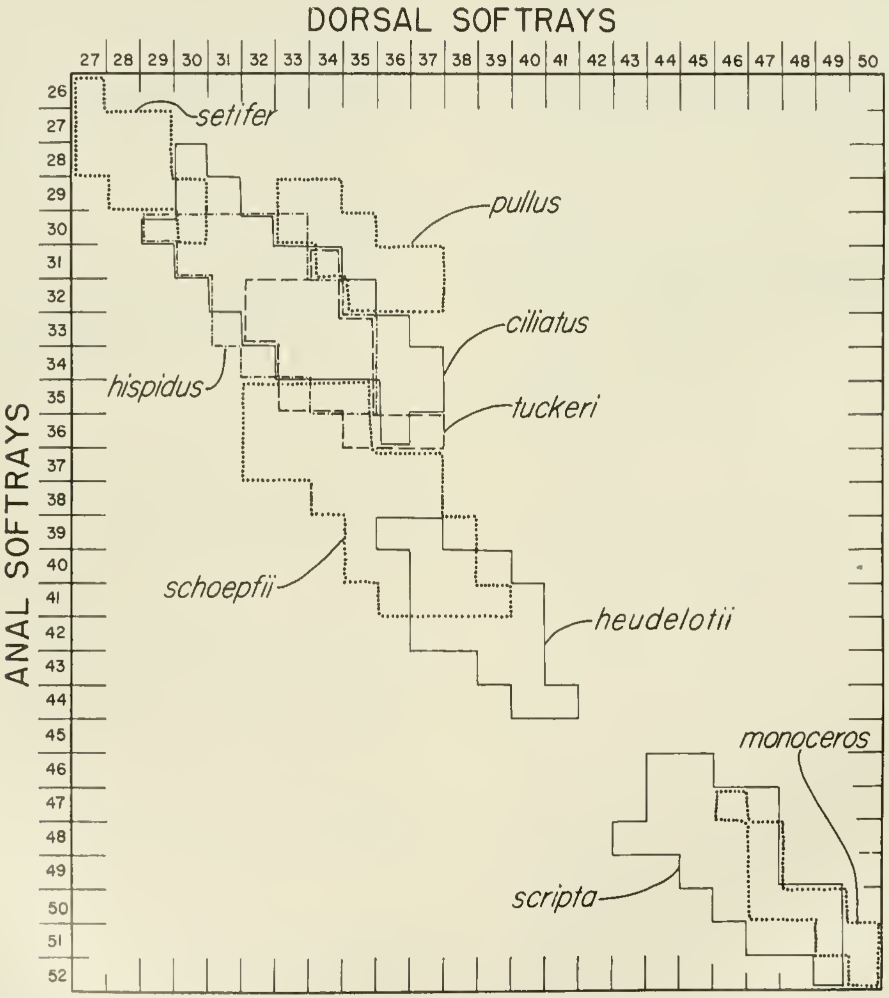

FIGURE 3.—Dorsal and anal soft ray correlation in western North Atlantic Monacanthidae. The various outlines (dots, dashes, solid lines, and dots and dashes) encompass the dorsal and anal ray combinations found in the nine species.

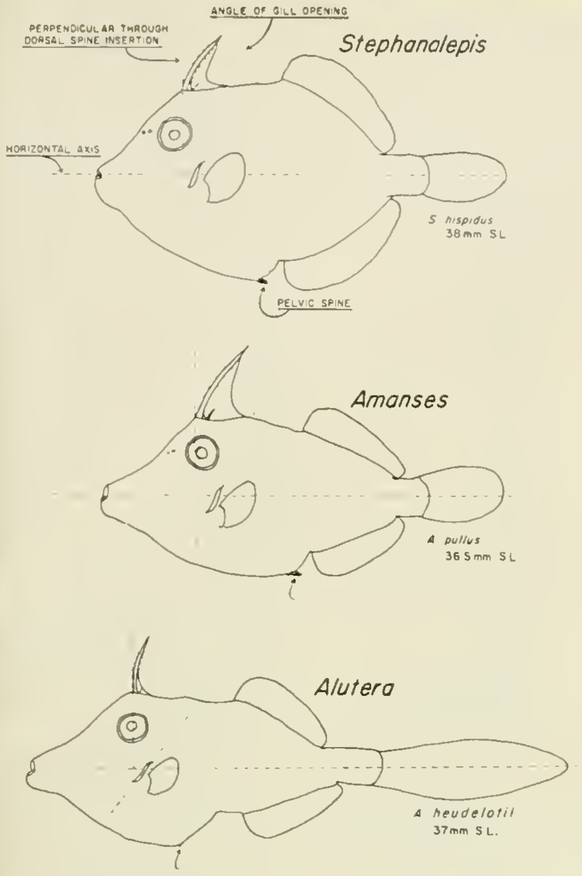

FIGURE 4.—Outlines of *Stephanolepis*, *Amanses*, and *Alutera*, illustrating location of the pelvic spine, positional relation of the first dorsal spine to the eye, and angle of the gill opening to the horizontal body axis.

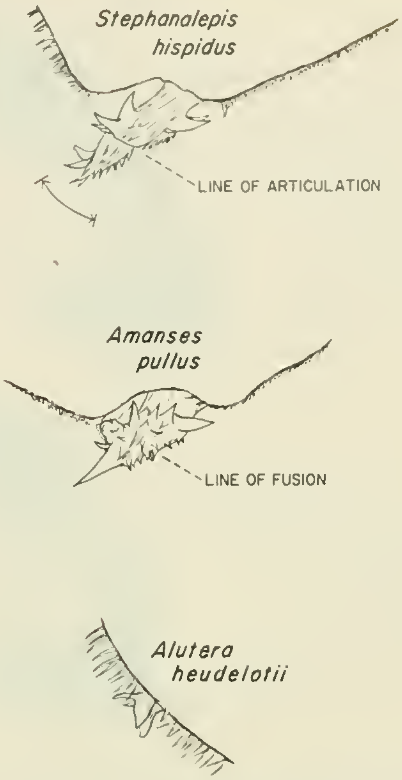

FIGURE 5.—Pelvic spines: *Stephanolepis hispidus*, 38 mm. S.L.; *Amanses pullus*, 36.5 mm. S.L.; and *Alutera heudelotii*, 37 mm. S.L. The ratio of magnification of the drawings is 1.0, 1.33, and 4.0.

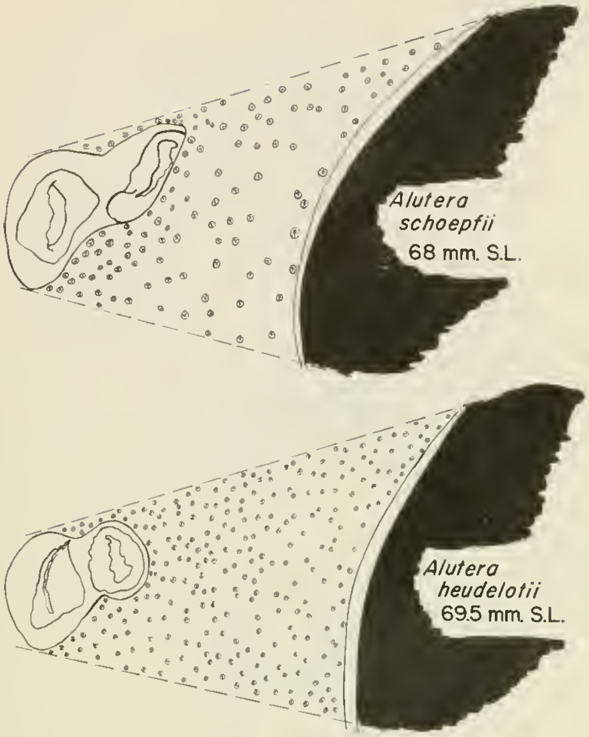

FIGURE 6.—Diagrammatic section of head region between eye and nostrils, illustrating the relative number and position of scale spines in this area: *Alutera schoepfii*, 68 mm. S.L.; *Alutera heudelotii*, 69.5 mm. S.L.

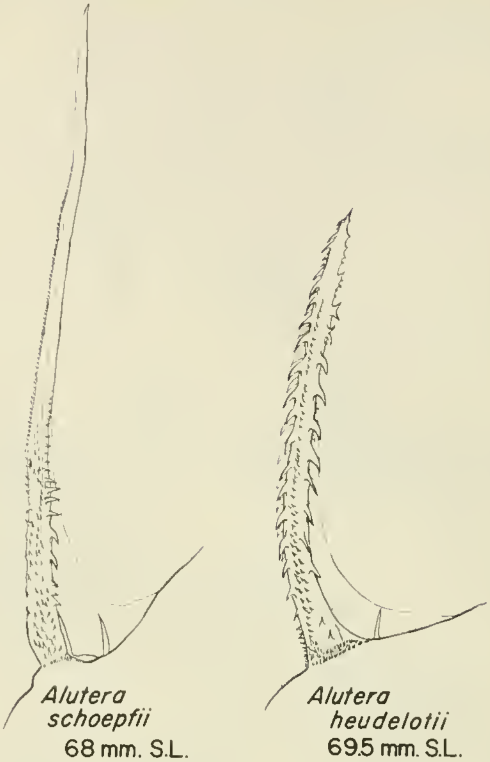

FIGURE 7.—Dorsal spines: *Alutera schoepfii*, 68 mm. S.L.; *Alutera heudelotii*, 69.5 mm. S.L.

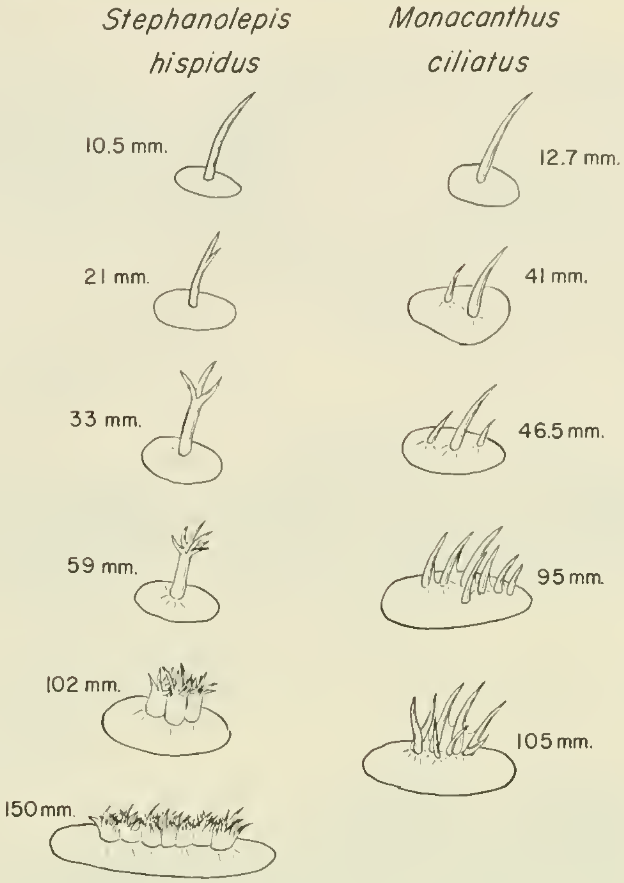

FIGURE 8.—Scales of *Stephanolepis hispidus* and *Monacanthus ciliatus*, illustrating development of the scale spines with increase in body size. The drawings are semidiagrammatic and are not drawn to the same relative proportion.

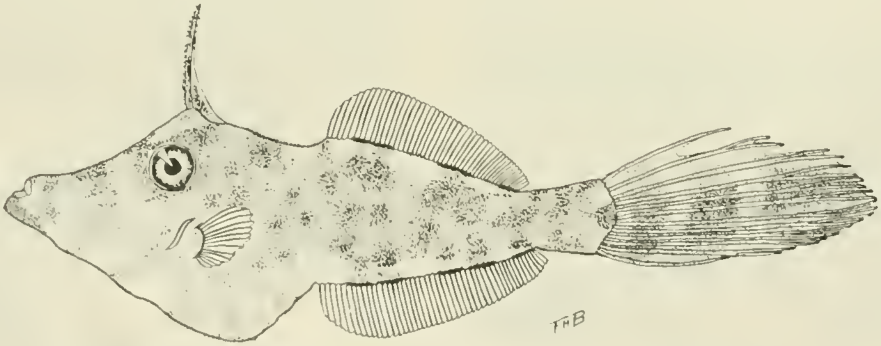

FIGURE 9.—*Alutera scripta*, 31.0 mm. S.L. (*Combat* station 438).

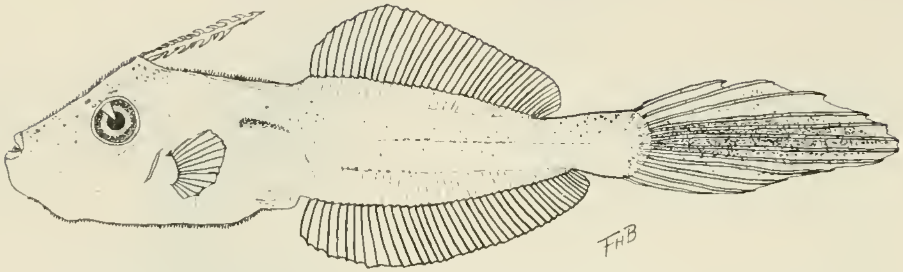

FIGURE 10.—*Alutera schoepfii*, 15.0 mm. S.L. (*Gill* cruise 2, regular station 5).

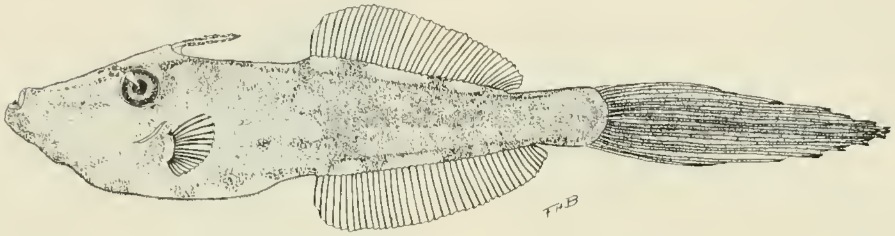

FIGURE 11.—*Alutera schoepfii*, 32.5 mm. S.L. (*Combat*, Port Canaveral, Fla.).

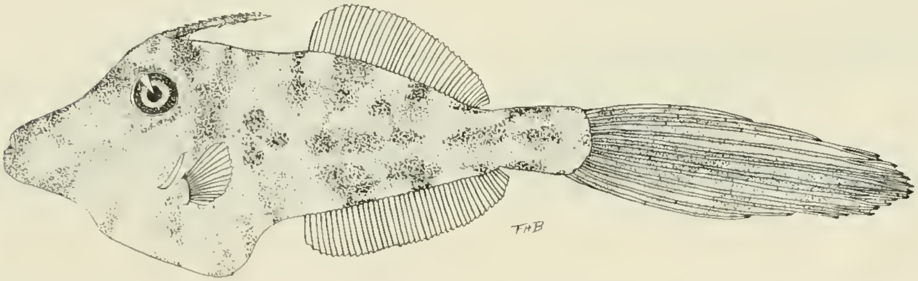

FIGURE 12.—*Alutera heudelotii*, 30.5 mm. S.L. (*Oregon* station 1074, University of Florida 3829).

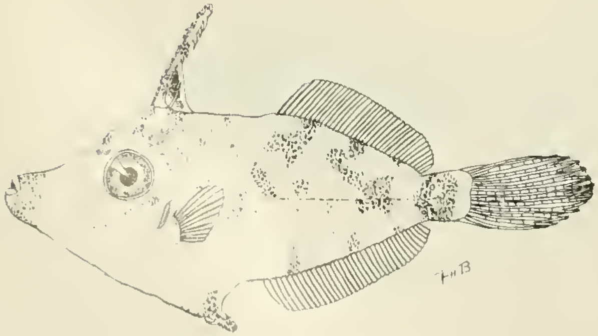

FIGURE 13.—*Monacanthus tuckeri*, 15.3 mm. S.L. (Academy of Natural Sciences of Philadelphia 84471).

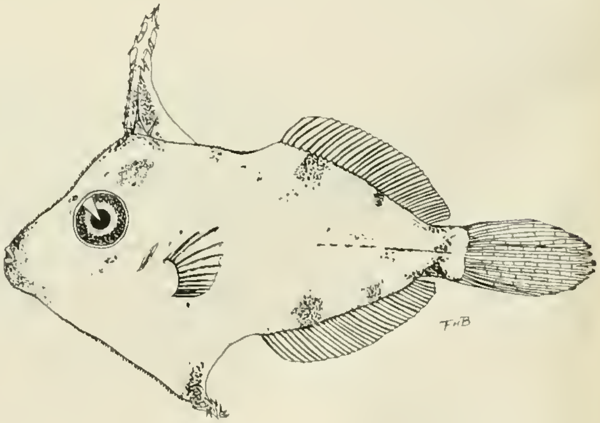

FIGURE 14.—*Monacanthus ciliatus*, 11.0 mm. S.L. (*Silver Bay* station 476).

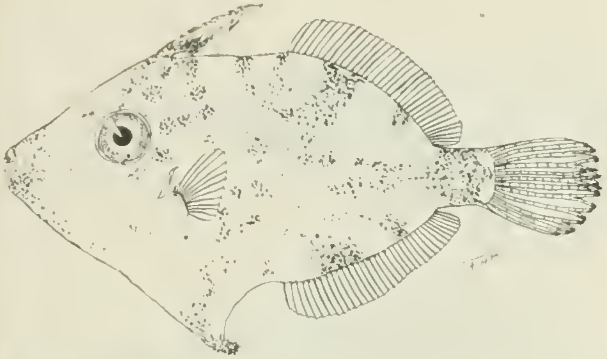

FIGURE 15.—*Monacanthus ciliatus*, 15.3 mm. S.L. (*Gill* cruise 7, regular station 54).

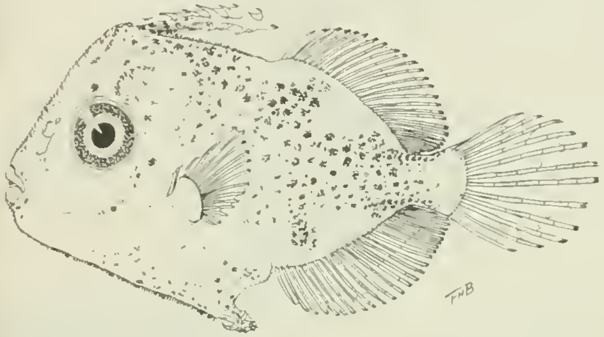

FIGURE 16.—*Stephanolepis hispidus*, 6.5 mm. S.L. (*Gill* cruise 7, regular station 38).

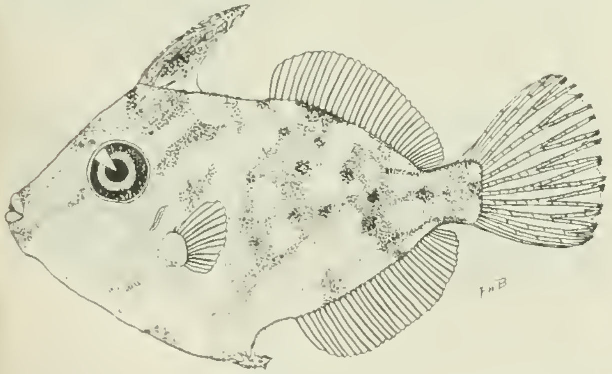

FIGURE 17.—*Stephanolepis hispidus*, 15.2 mm. S.L. (*Gill* cruise 8, regular station 48).

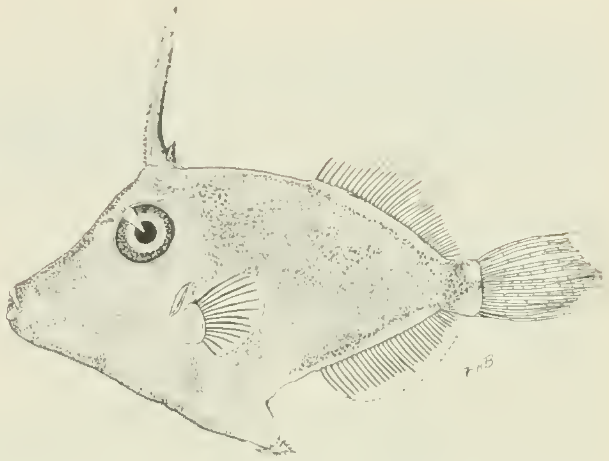

FIGURE 18.—*Amanses pullus*, 17.5 mm. S.L. (*Gill* cruise 9, from stomach contents of *Katsuwonus pelamis*, Nov. 15, 1954; 1600).

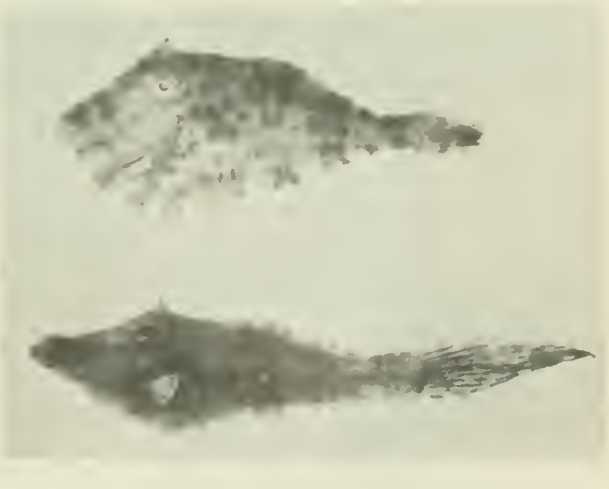

FIGURE 19.—Top: *Alutera monoceros*, 53 mm. S.L. (U.S. National Museum 117022). Bottom: *Alutera scripta*, 53 mm. S.L. (*Gill* cruise 8, regular station 52).

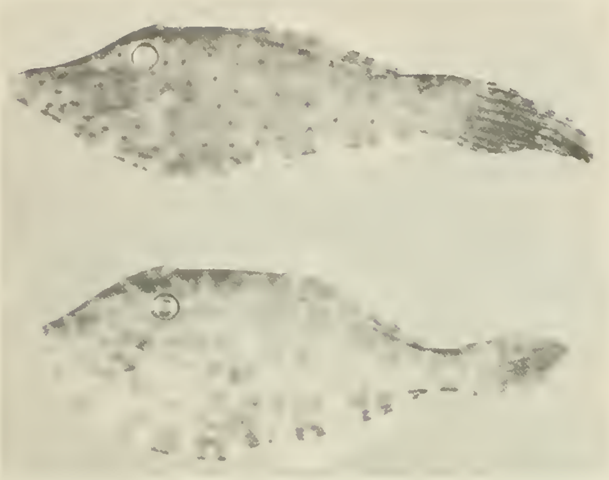

FIGURE 20.—Top: *Alutera scripta*, 119 mm. S.L. Bottom: *Alutera monoceros*, 122 mm. S.L. (Both from *Combat* station 459.) Note differences in body depth, caudal peduncle, and caudal-fin length.

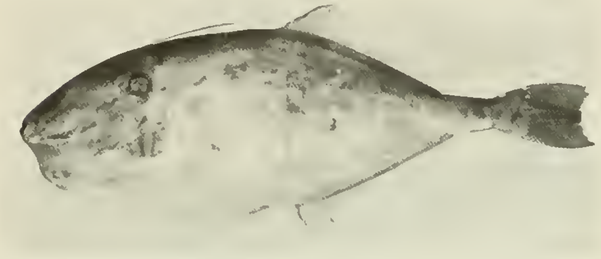

FIGURE 21.—*Alutera monoceros*, 545 mm. S.L. (*Silver Bay* station 1550).

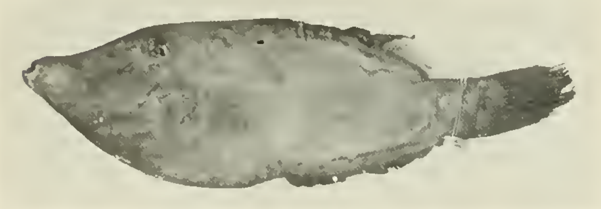

FIGURE 22.—*Alutera scripta*, 377 mm. S.L. (U.S. National Museum 170118).

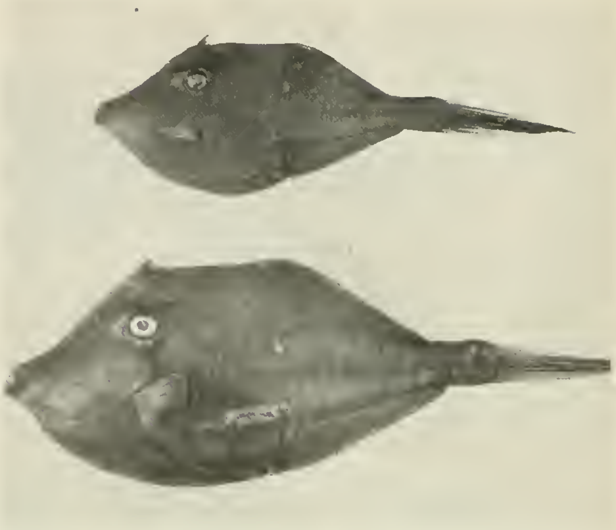

FIGURE 23.—*Alutera schoepfii*. Top: 126 mm. S.L. (University of Florida 2542). Bottom: 176 mm. S.L. (University of Florida C–9–2053–3). Body pigment spots that are frequently present on *A. schoepfii* of this size are not present on these two specimens.

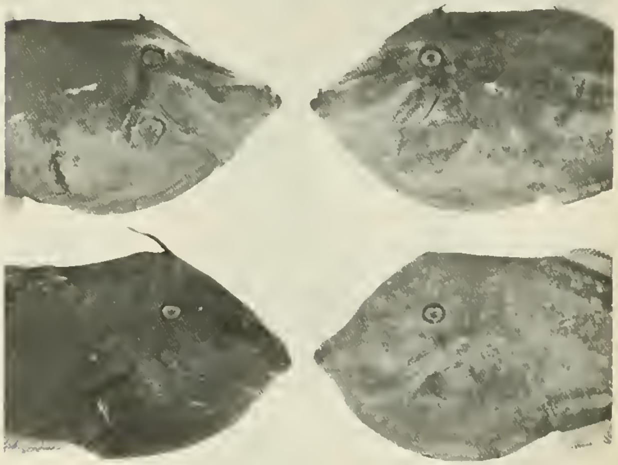

FIGURE 24.—*Alutera schoepfii*, 317 to 343 mm. S.L. (Tulane University 17106). Note variations in head profile and in size and position of the eye in this species.

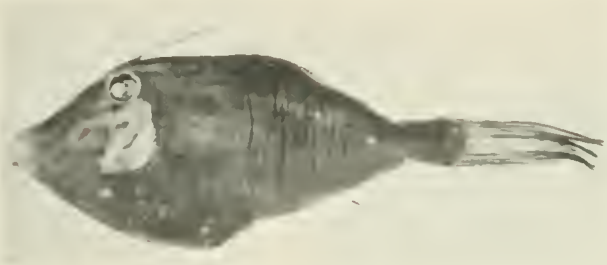

FIGURE 25.—*Alutera heudelotii,* 230 mm. S.L. (Tulane University 16316). Note the small distance from eye to dorsal spine.

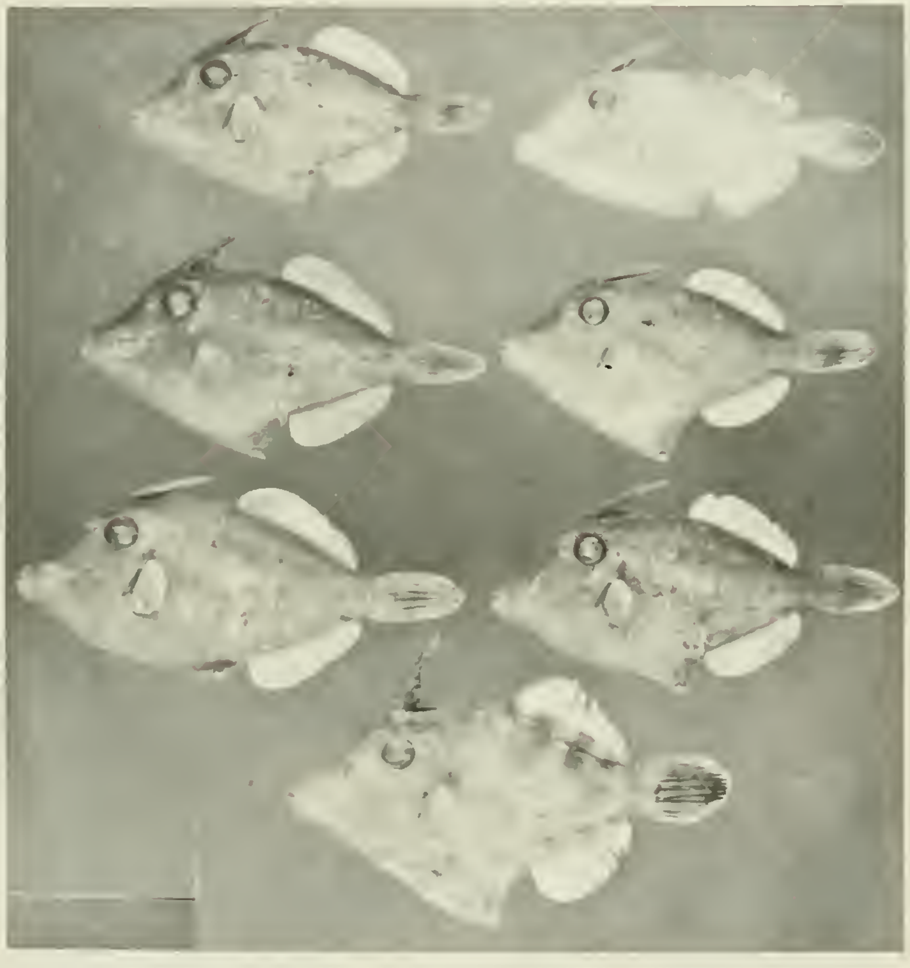

FIGURE 26.—*Amanses pullus,* 45.5 to 58 mm. S.L. (*Combat* station 474). Note variation in pigmentation.

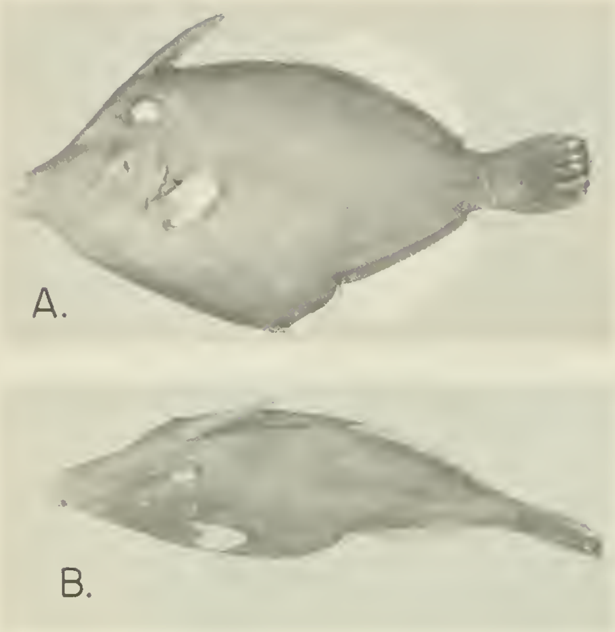

FIGURE 27.—*Amanses pullus*, 158 mm. S.L. female (University of Florida 7266). A. Lateral view. B. Oblique view showing deep groove behind dorsal spines.

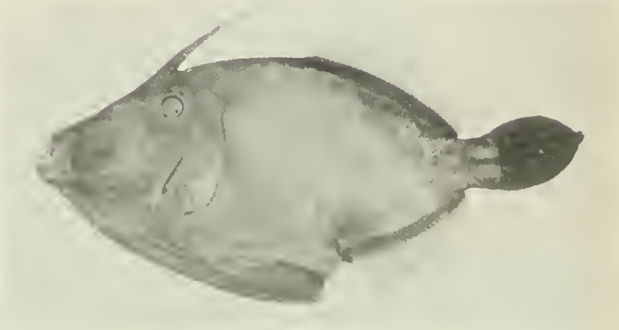

FIGURE 28.—*Amanses pullus*, 322 mm. S.L. male (U.S. National Museum 32096). Note prominent patch of bristles and pairs of large recurved spines on peduncle.

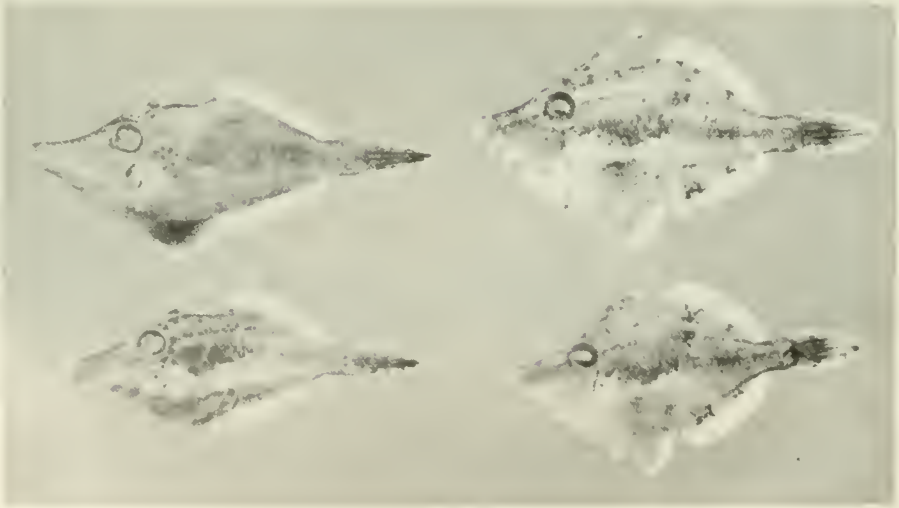

FIGURE 29.—Left, *Monacanthus tuckeri*. Top: 56.5 mm. S.L. male. Bottom: 49 mm. S.L. female. (Both Academy of Natural Sciences of Philadelphia 84478.) Right, *Monacanthus ciliatus*. Top: Immature specimen, 54 mm. S.L. Bottom: Immature specimen, 47.5 mm. S.L. (Both from Sanibel Island, Fla., August 19, 1959.) Note black line on ventral flap of the male *M. tuckeri* and compare body profiles of the two species at similar sizes.

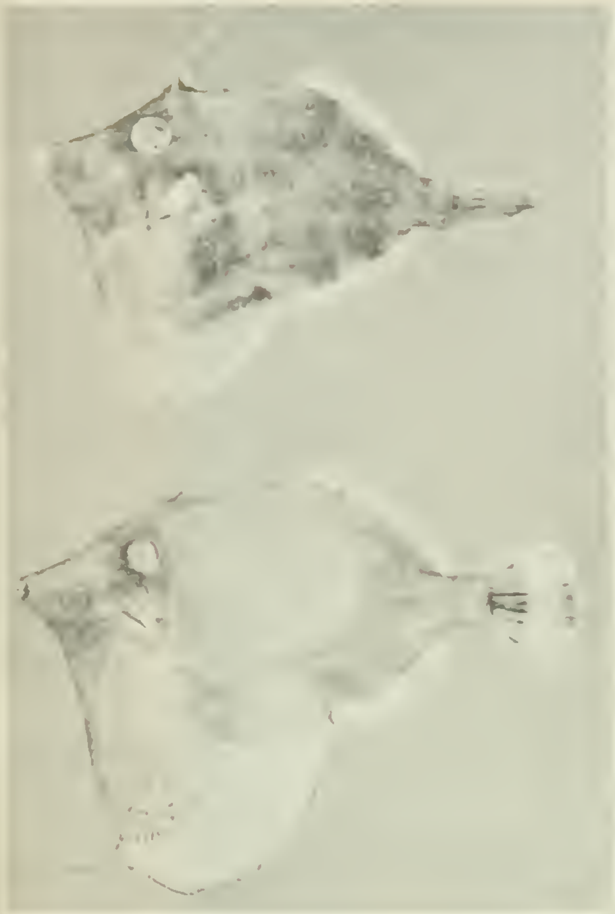

Figure 30.—*Monacanthus ciliatus*. Top: 92.5 mm. S.L. female. Bottom: 103 mm. S.L. male. (Both University of Florida 3611.) Note larger, recurved spines on caudal peduncle and black line on margin of ventral flap of male.

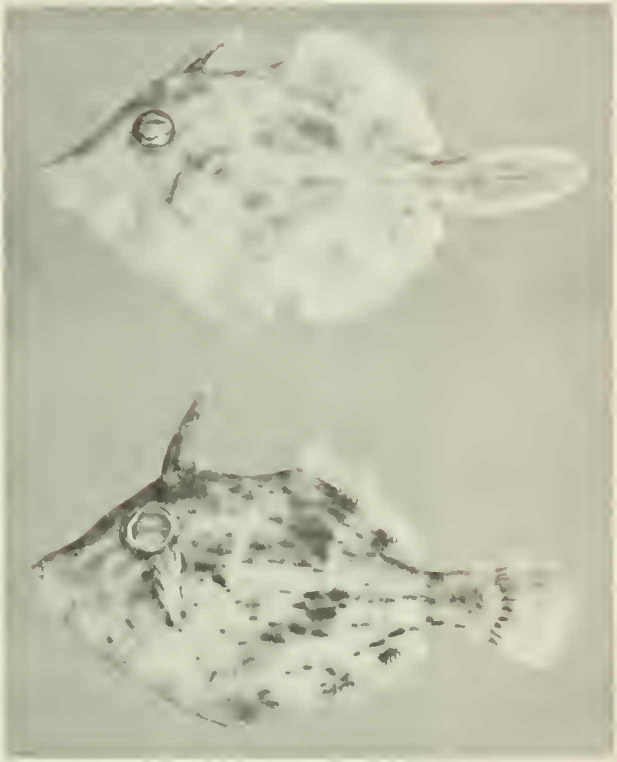

Figure 31.—Top: *Stephanolepis hispidus*, 52.5 mm. S.L. (*Gill* cruise 4, regular station 46). Bottom: *Stephanolepis setifer*, 55 mm. S.L. (*Combat* station 459). Note small spots and dashes of pigment and bars on caudal fin of *S. setifer*.

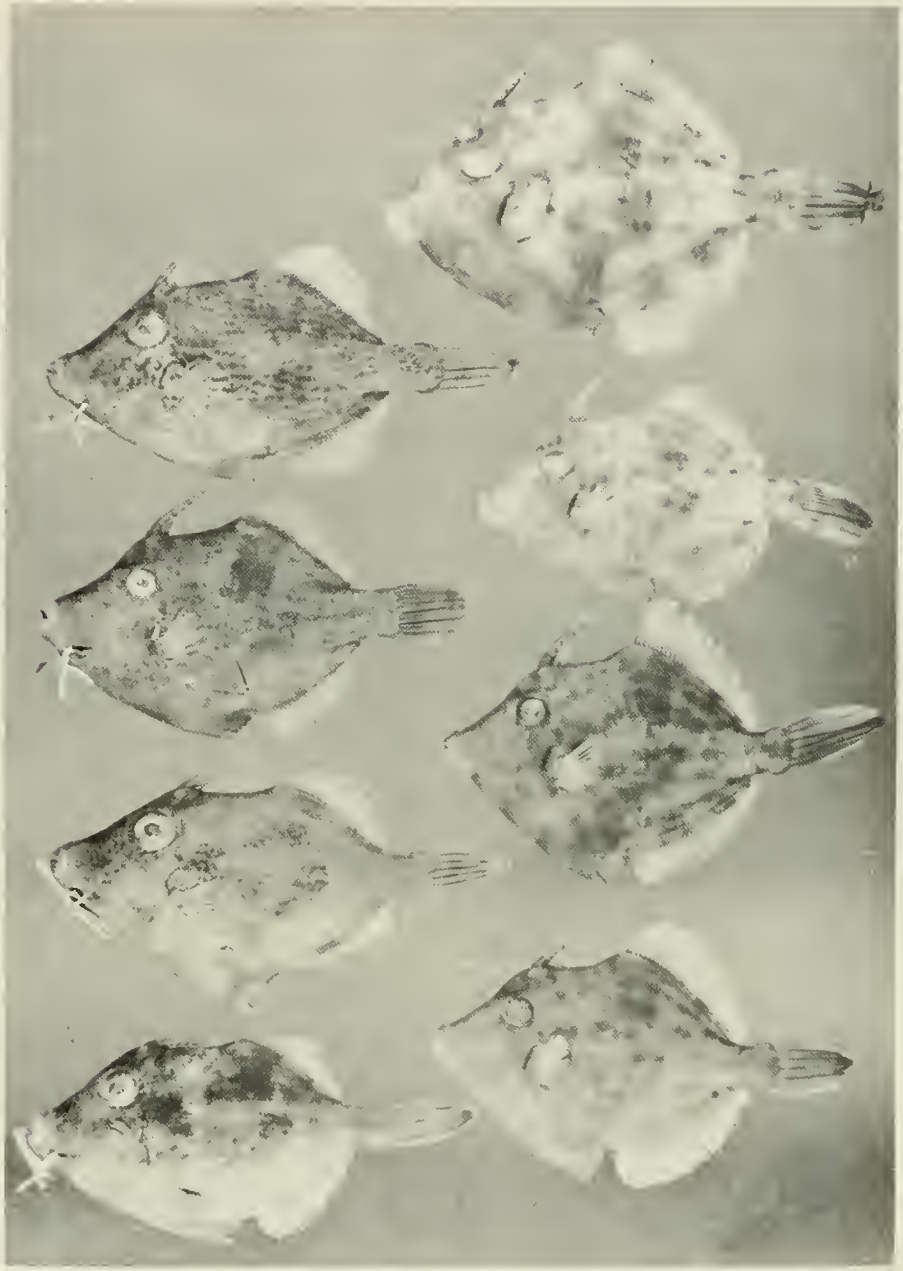

Figure 32.—Left: *Stephanolepis setifer* (Stanford University Natural History Museum 4772). Standard length and sex from top to bottom, 101-mm. male, 95-mm. male, 98-mm. female, 96-mm. female. Right: *Stephanolepis hispidus*, immature specimens (top two, *Silver Bay* station 1315, bottom two, University of Florida No. C–7–1253–4). Standard lengths from top to bottom, 103, 83.5, 88.5, and 88 mm. Note intraspecific and interspecific variation in size of eye. The elongated second ray of the two males of *S. setifer* is not clearly shown.

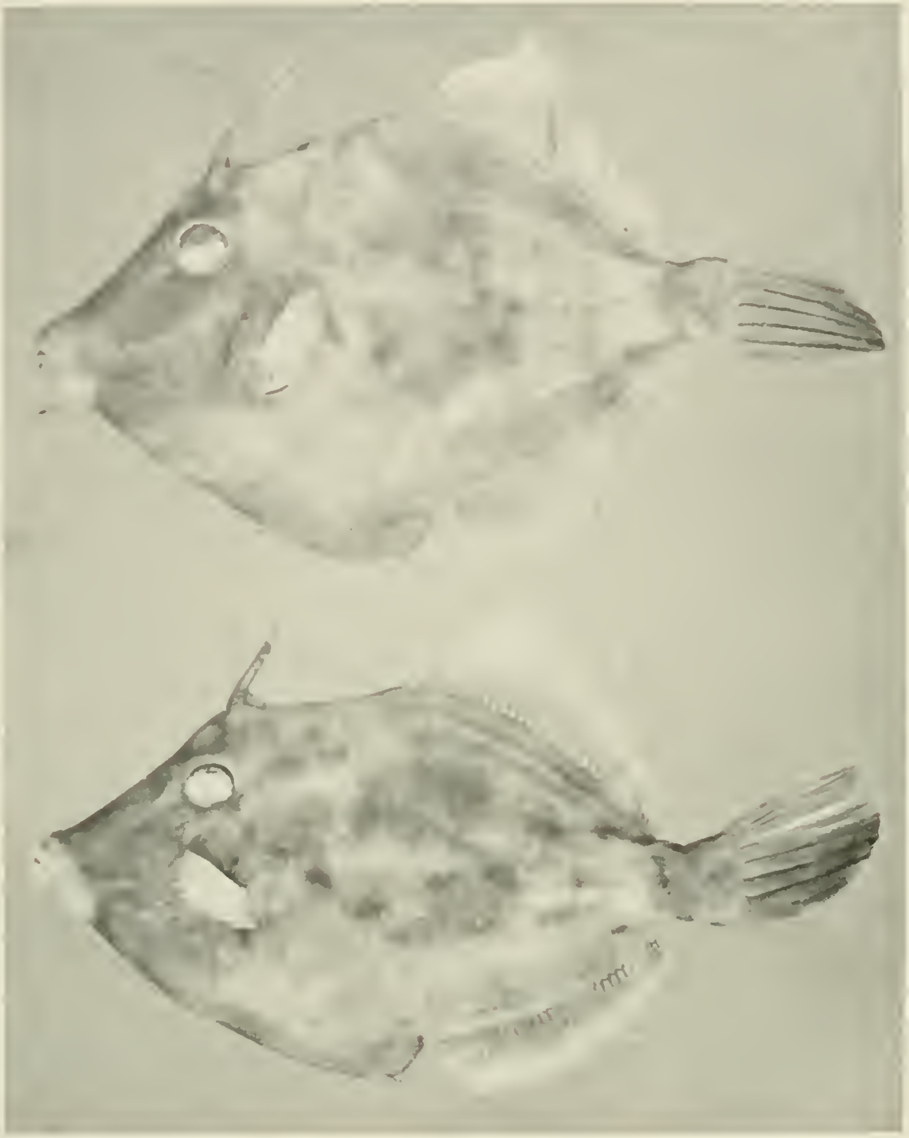

FIGURE 33.—*Stephanolepis hispidus.* Top: 167 mm. S.L. female (*Silver Bay* station 1297). Bottom: 169 mm. S.L. male (*Silver Bay* station 1210). Note the elongated second dorsal ray and patch of caudal peduncle bristles on the male, absent on the female.

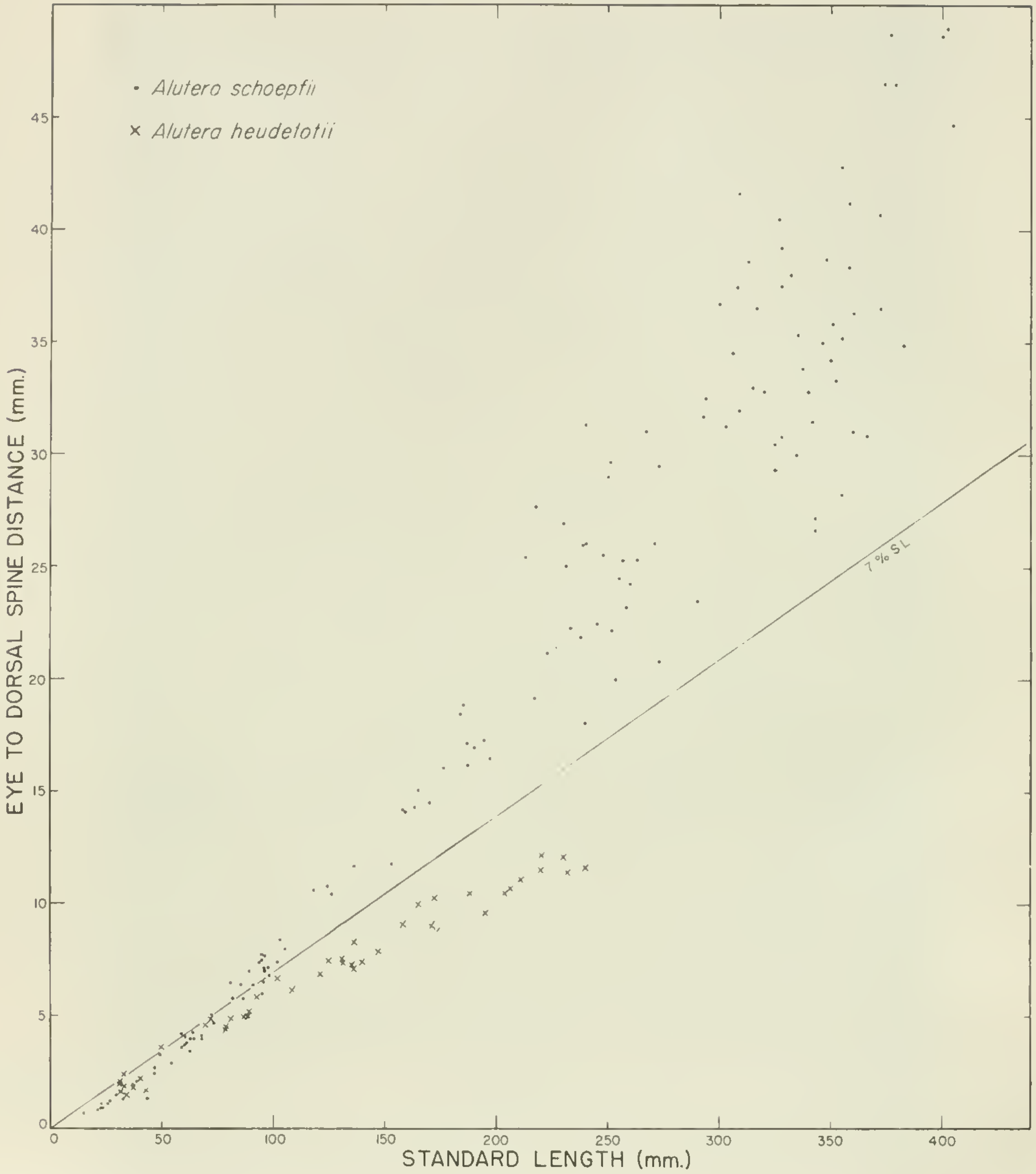

FIGURE 34.—Relation of eye to dorsal-spine distance and standard length for *Alutera schoepfii* and *Alutera heudelotii*. Specimens larger than 100 mm. can be distinguished by this character.

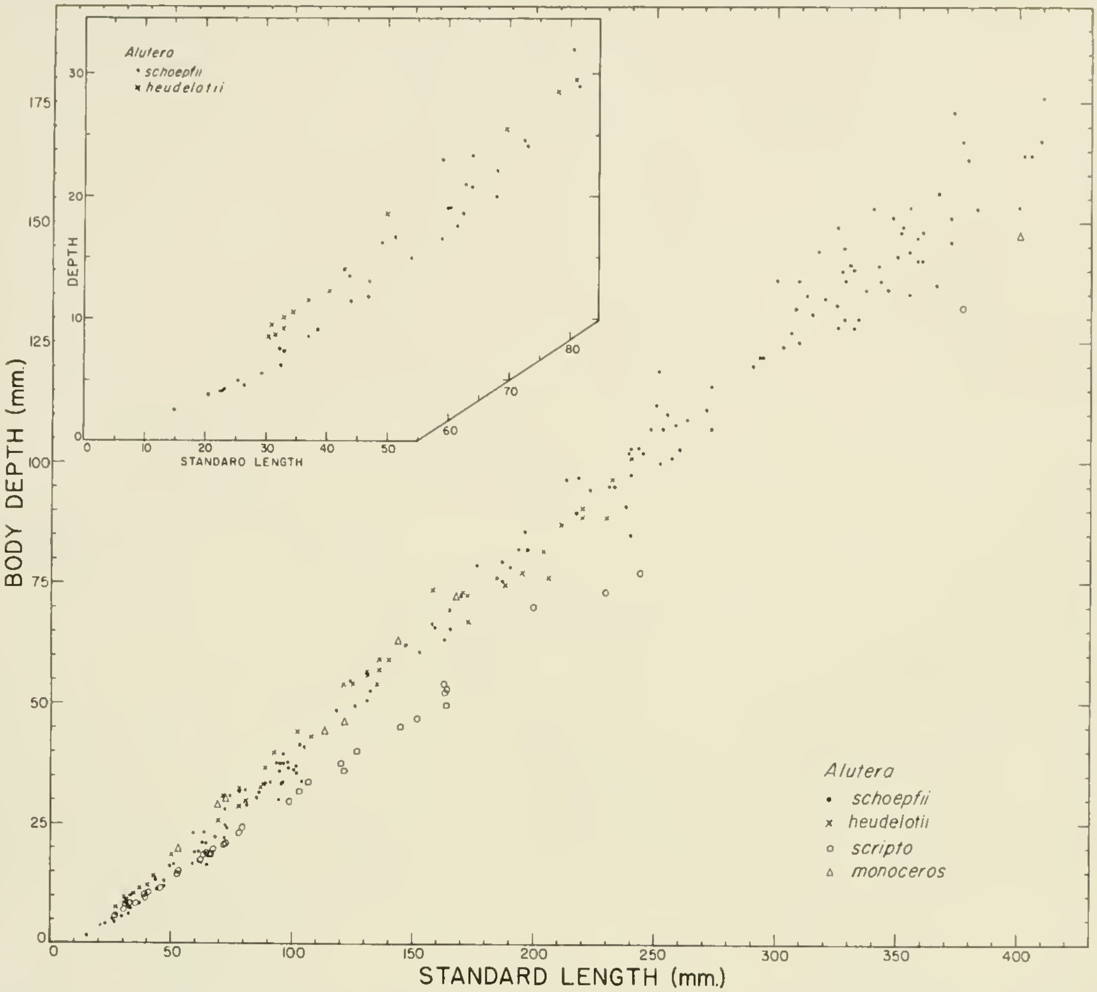

FIGURE 35.—Relation of body depth to standard length for *Alutera schoepfii*, *Alutera heudelotii*, *Alutera scripta*, and *Alutera monoceros*. Insert graph illustrates difference in depth between *Alutera schoepfii* and *Alutera heudelotii* at sizes less than about 35 mm.

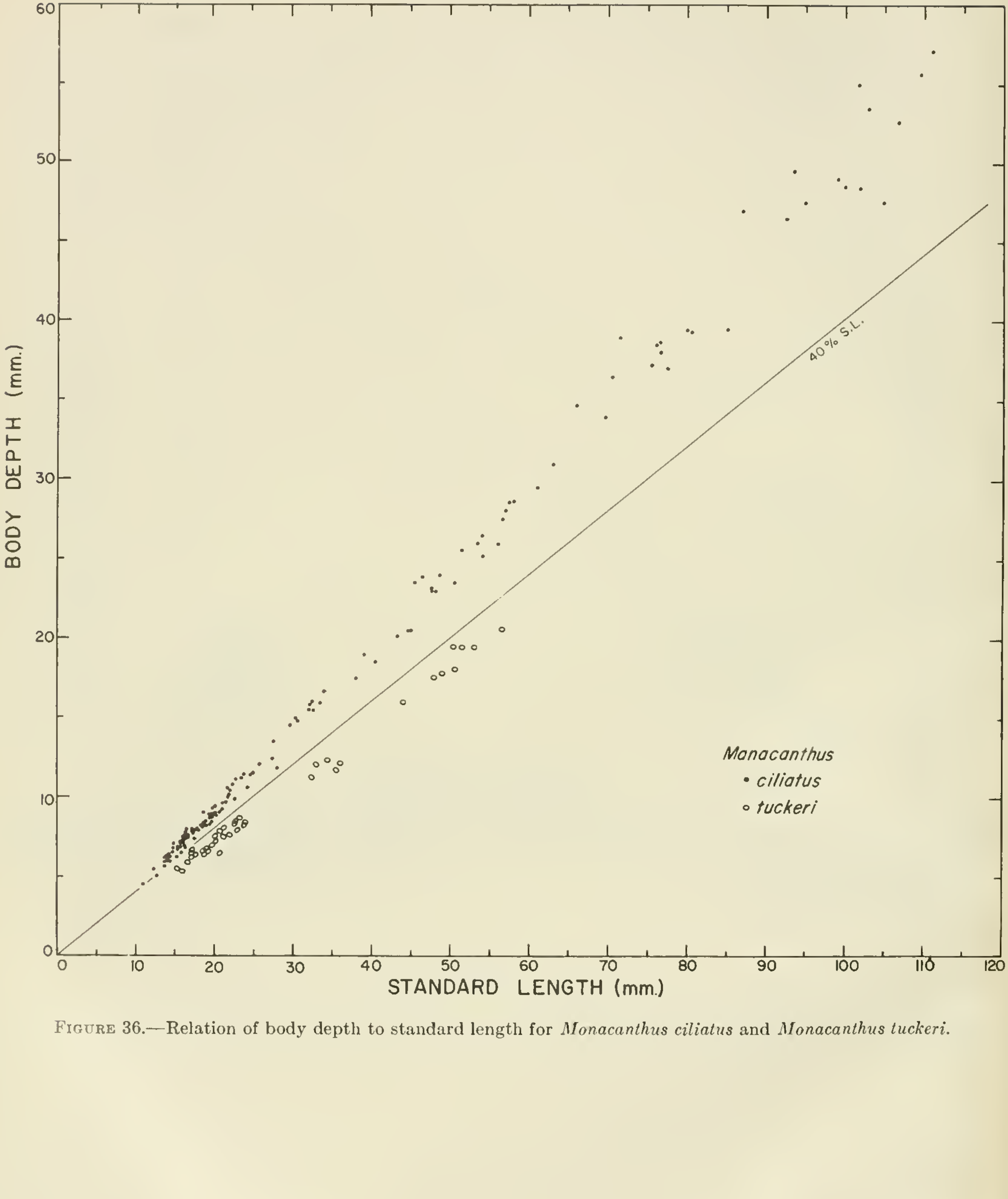

FIGURE 36.—Relation of body depth to standard length for *Monacanthus ciliatus* and *Monacanthus tuckeri*.

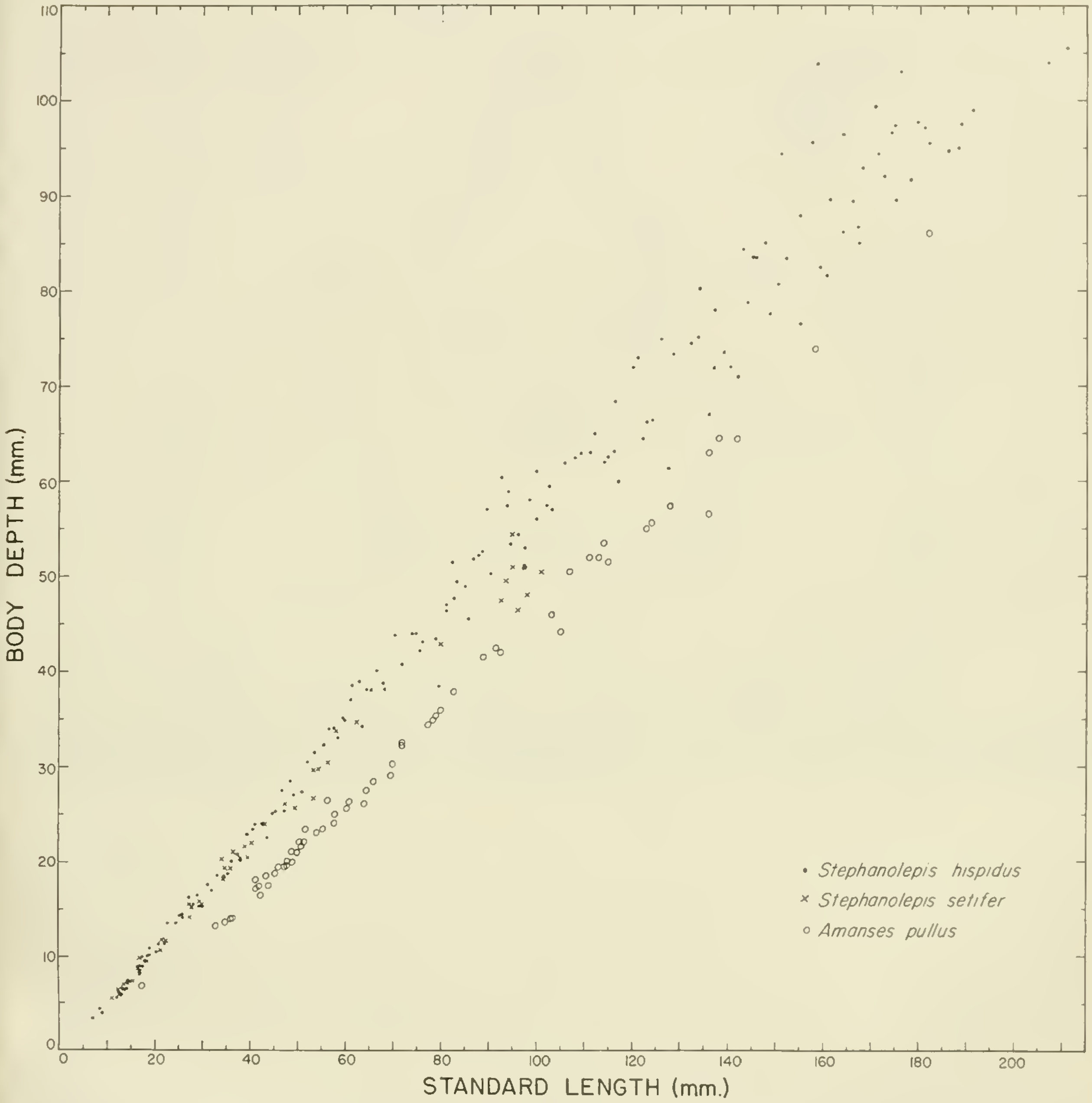

Figure 37.—Relation of body depth to standard length for *Stephanolepis hispidus*, *Stephanolepis setifer*, and *Amanses pullus*.

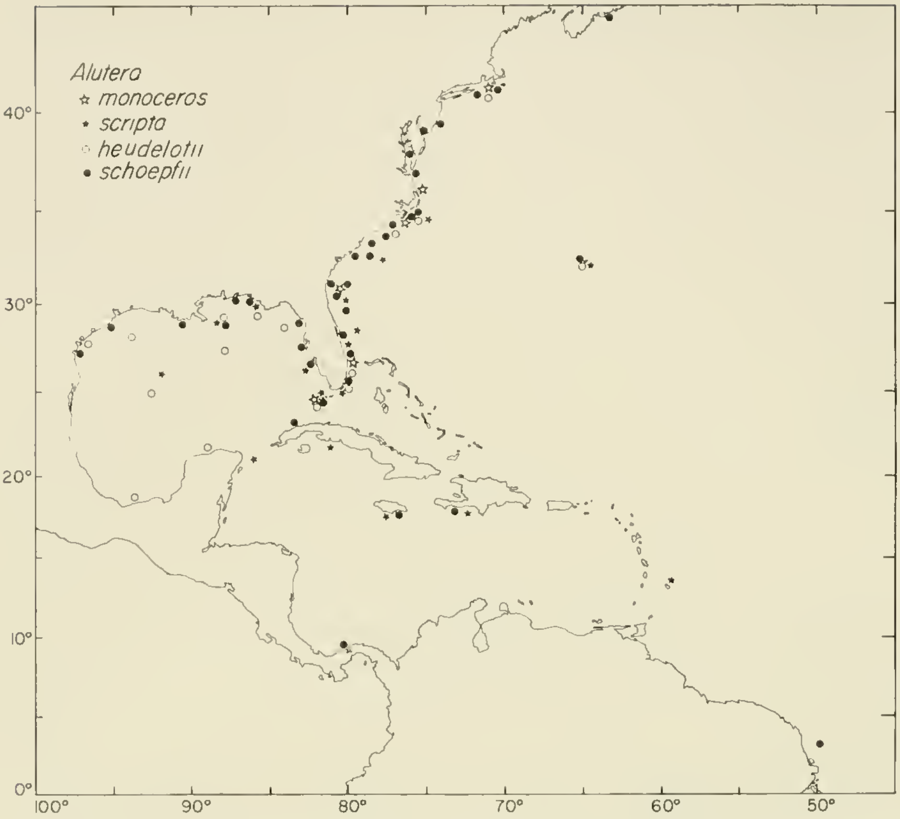

FIGURE 38.—General distribution of specimens examined of *Alutera monoceros*, *Alutera scripta*, *Alutera heudelotii*, and *Alutera schoepfii*.

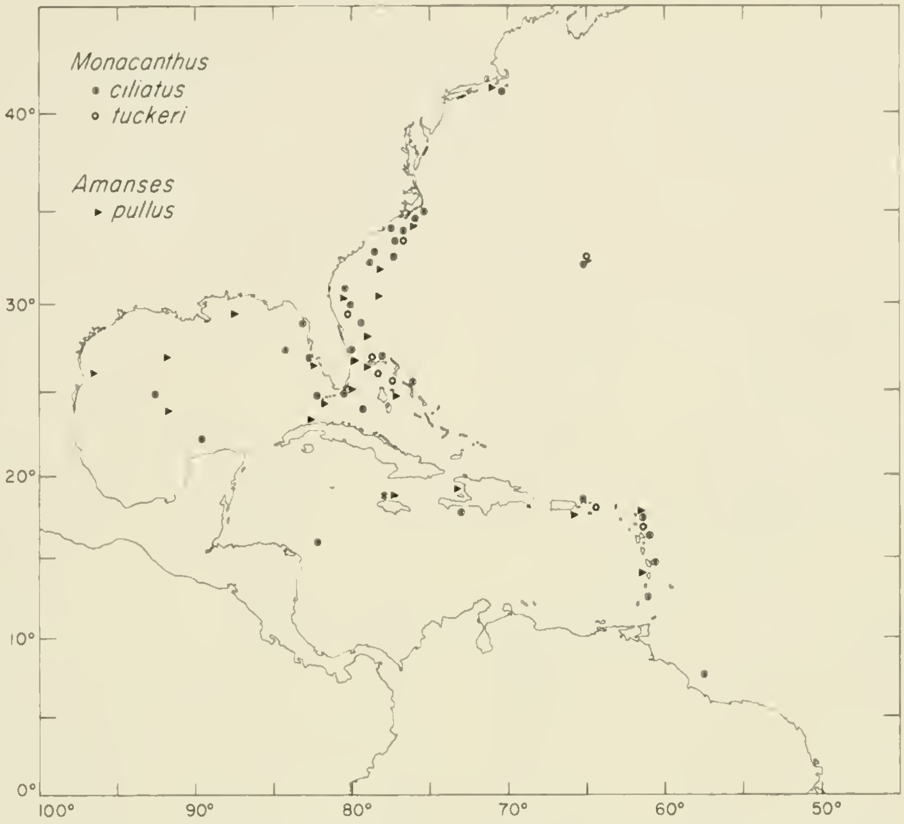

FIGURE 39.—General distribution of specimens examined of *Monacanthus ciliatus*, *Monacanthus tuckeri*, and *Amanses pullus*.

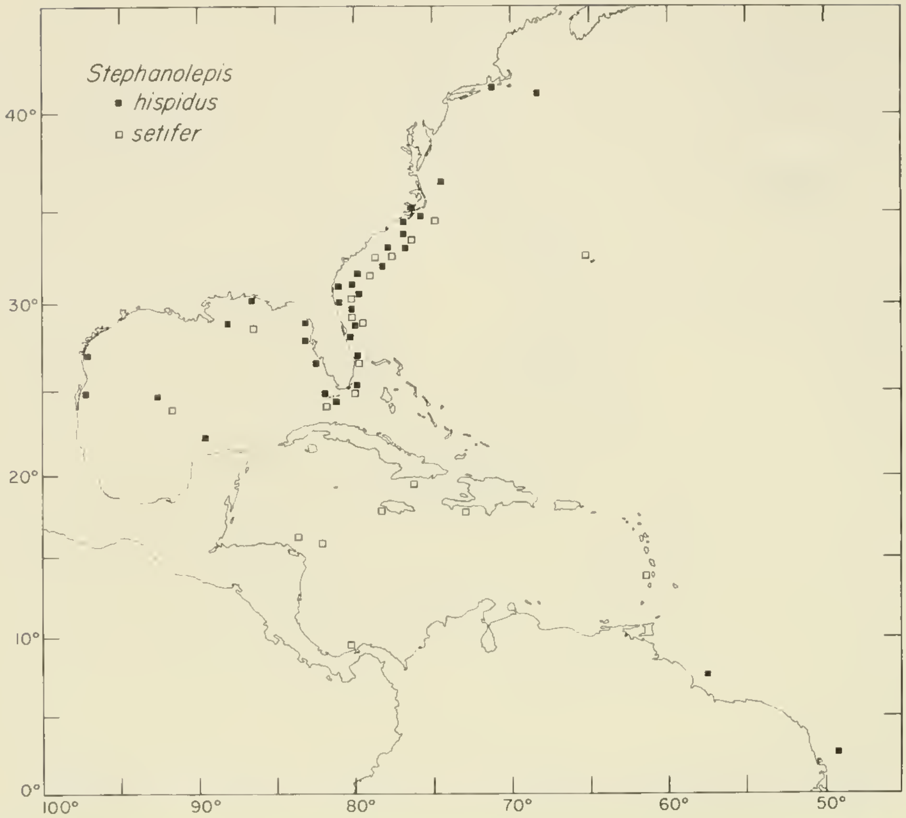

FIGURE 40.—General distribution of specimens examined of *Stephanolepis hispidus* and *Stephanolepis setifer*. (No attempt has been made to indicate all records where collecting stations were closely spaced.)

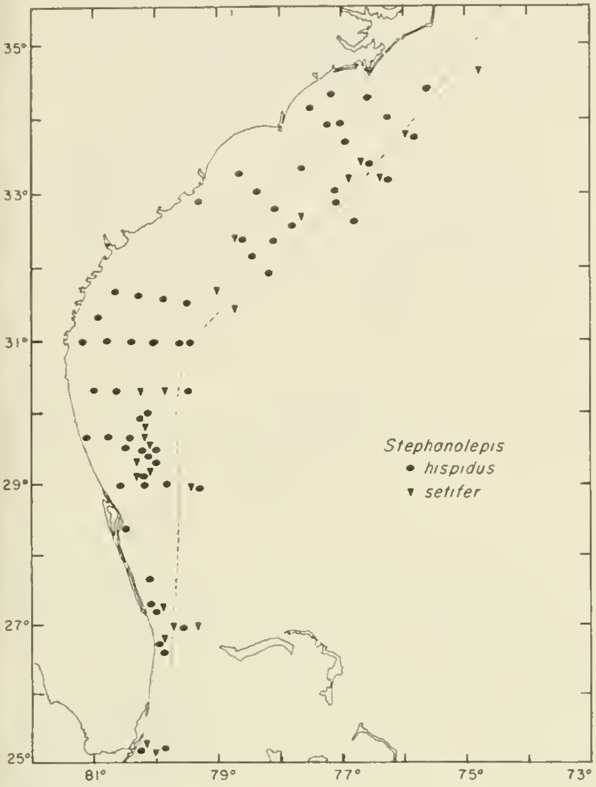

FIGURE 41.—Locations of specimens of *Stephanolepis hispidus* and *Stephanolepis setifer* taken at the surface off the southeastern Atlantic coast of the United States by dip net and meter larvae net on cruises of the *Gill*, *Combat*, and *Silver Bay*. The 20-fathom contour line is represented by the line of dots. The approximate axis of the Gulf Stream is represented by the line of dashes.

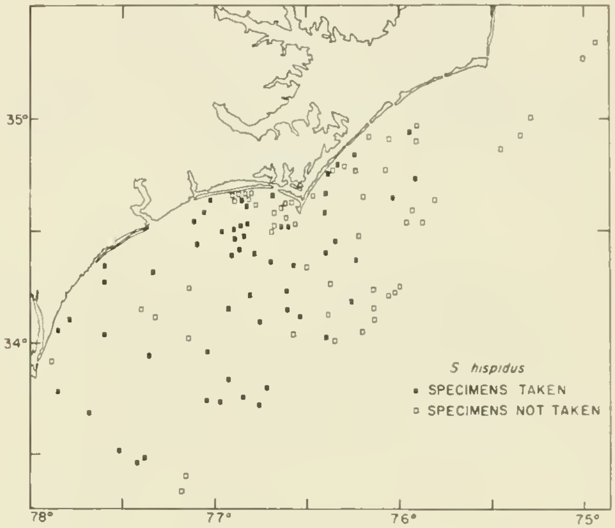

FIGURE 42.—Chart of the waters off North Carolina showing the concentrated bottom-trawling stations made by the *Silver Bay* in September 1959 and indicating the stations at which *Stephanolepis hispidus* was taken (black squares) and was not taken (open squares).

B. TABLES

Table 1.—*Dorsal ray–anal ray relation for 10 specimens of* Alutera monoceros

Dorsal soft rays

Anal soft rays	46	47	48	49	50
47	1				
48		2			
49					
50		1	2	1	
51				1	1
52					1

Table 2.—*Dorsal ray–anal ray relation for 47 specimens of* Alutera scripta

Dorsal soft rays

Anal soft rays	43	44	45	46	47	48	49
46		1	2				
47		1	1		1		
48	1			5	3		
49			2	7	8		
50				3	2	4	2
51					1	2	
52							1

Table 3.—*Dorsal ray–anal ray relation for 125 specimens of* Alutera schoepfii

Dorsal soft rays

Anal soft rays	32	33	34	36	36	37	38	39
35	1		2	1				
36		1	2	1				
37	1	2	2	3	6	1		
38			3	9	15	2		
39				7	17	11	1	
40				2	9	9	5	
41					1	2	7	2

Table 4.—*Dorsal ray–anal ray relation for 58 specimens of* Alutera heudelotii

Dorsal soft rays

Anal soft rays	36	37	38	39	40	41
39	1	2				
40		3	8	4		
41		3	10	7	1	
42		2	3	10	1	
43				1		
44					1	1

Table 5.—*Dorsal ray–anal ray relation for 52 specimens of* Monacanthus tuckeri

Dorsal soft rays

Anal soft rays	32	33	34	35	36	37
31			1			
32	1		1			
33	2	3	2	1		
34		1	11			
35		1	9	9	2	
36			1	1	4	2

Table 6.—*Dorsal ray–anal ray relation for 239 specimens of* Monacanthus ciliatus

Dorsal soft rays

Anal soft rays	29	30	31	32	33	34	35	36	37
28		6							
29		23	10						
30	2	14	30	12					
31		2	13	22	5	2			
32			1	10	8	17	5		
33				2	4	16	9	3	
34					1	3	5	6	1
35								4	1
36								2	

Table 7.—*Dorsal ray–anal ray relation for 975 specimens of* Stephanolepis hispidus

Dorsal soft rays

Anal soft rays	29	30	31	32	33	34	35
30	1	3	18	3	1		
31		4	67	97	3		
32			21	216	154	6	
33			1	37	209	17	2
34				1	13	38	6
35						3	5

Table 8.—*Dorsal ray–anol ray relation for 133 specimens of* Stephanolepis setifer

Dorsal soft rays

Anal soft rays	27	28	29	30
26	2			
27	18	16	1	
28	6	50	8	
29		6	20	2
30				4

FIGURE 9.—*Dorsal ray–anal ray relation for 81 specimens of* Amanses pullus

Anal soft rays	Dorsal soft rays 33	34	35	36	37
29	2	1			
30	2	13	4		
31		12	32	4	1
32			5	4	1

TABLE 10.—*Dorsal ray–anal ray relation for 133 specimens of* Stephanolepis setifer *and 975 specimens of* Stephanolepis hispidus

[s=*S. setifer;* h=*S. hispidus;* figures are the percentages of the total for each ray combination]

Anal soft rays	Dorsal soft rays 27	28	29	30	31	32	33	34	35
26	s 1.5								
27	s 13.5	s 12.0	s 0.8						
28	s 4.5	s 37.7	s 6.0						
29		s 4.5	s 15.0	s 1.5					
30			h 0.1	s 3.0 h 0.3	h 1.8	h 0.3	h 0.1		
31				h 0.4	h 6.9	h 9.9	h 0.3		
32					h 2.2	h 22.3	h 15.8	h 0.6	
33					h 0.1	h 3.8	h 21.4	h 6.9	h 0.2
34						h 0.1	h 1.3	h 3.9	h 0.5
35								h 0.3	h 0.5

TABLE 11.—*Numbers of pectoral soft rays in western North Atlantic Monacanthidae*

[Counts of rays from both sides; not recorded with respect to right and left sides; rudimentary pectoral spine not included in counts]

Species	9–10	10–10	10–11	11–11	11–12	12–12	12–13	13–13	13–14	14–14	14–15	15–15
Alutera monoceros										10		
Alutera scripta								2	2	41	2	2
Alutera schoepfii					6	63	23	61	3	2		
Alutera heudelotii							3	40	9	8		
Monacanthus tuckeri			3	34		2						
Monacanthus ciliatus	1	4	18	148	10	11	1					
Stephanolepis hispidus						5	10	236	42	63		
Stephanolepis setifer				19	16	88	4					
Amanses pullus							3	54	8	13		

TABLE 12.—*Relation of body depth to standard length in Monacanthidae of the western north Atlantic, by species and millimeter intervals*

[In percent of standard length for grouped millimeter intervals of standard length]

Standard length (mm.)	Body depth in percent of standard length								
	Alutera				*Monacanthus*		*Stephonolepis*		*Amanses pullus*
	monaceras	*scripta*	*schoepfii*	*heudelotii*	*tuckeri*	*ciliatus*	*hispidus*	*setifer*	
0–4.9									
5–9.9							43.3–48.6		
10–14.9						39.1–48.6	46.2–51.7	47.2–52.2	
15–19.9			17.3		33.1–38.5	39.9–48.5	48.7–57.9	48.4–57.8	38.9
20–24.9			18.2–18.5		31.3–37.9	43.2–48.8	51.2–58.7	50.2–54.6	
25–29.9		21.6	17.4–22.2	27.8		42.1–49.6	51.2–59.6	51.8–56.6	
30–34.9		22.6–24.5	19.1–23.2	27.6–30.6	34.5–36.4	47.7–49.5	52.8–55.7	51.7–59.6	40.3
35–39.9		23.1–25.9	22.7–23.9	31.1	33.0–33.9	46.1–48.7	52.9–58.0	52.0–57.3	38.6–39.1
40–44.9		25.9	25.9–30.9	30.1–32.6	36.4	45.7–46.8	51.3–58.0	54.3–56.3	38.8–44.2
45–49.9		25.2	25.1–33.1		36.3–36.5	45.6–51.9	53.9–59.0	51.9–54.9	40.8–43.3
50–59.9	36.8	27.4–28.0	27.8–39.0	37.0	35.8–38.6	46.4–49.9	53.4–60.0	50.4–58.6	41.8–46.9
60–69.9	42.0	27.7–29.2	25.2–36.4	36.7		48.4–52.6	53.9–62.6	52.7–55.7	40.8–43.2
70–79.9	41.4	28.8–30.2	30.0–40.4	36.2–42.9		47.7–54.5	48.3–62.2	55.5–58.4	43.3–45.1
80–89.9			35.6–39.8	36.4–41.0		46.5–54.0	54.8–63.6	49.1–55.9	45.1–46.6
90–99.9		30.0	29.6–41.1	43.0		49.5–52.9	54.4–65.2	48.4–56.8	45.4–46.2
100–124.9	37.7–38.6	29.5–31.4	32.4–44.0	39.8–44.5		45.2–54.5	51.3–61.0	46.8–50.9	42.1–47.2
125–149.9	43.8	31.0–31.5	38.5–40.1	40.0–43.4			49.3–60.1		41.5–46.7
150–174.9	43.1	30.2–33.1	38.8–42.6	38.7–46.5			49.4–65.8		46.8
175–199.9			40.4–44.7	39.5–39.6			50.4–58.2		47.3
200–224.9		35.0	41.2–45.3	36.8–41.2			50.0–50.2		
225–249.9		31.6–31.7	35.4–43.1	38.5–42.1					
250–274.9			38.2–47.4						
275–299.9			41.4						49.3
300–349.9			38.6–46.0						46.9–48.3
350–399.9		35.0	37.4–46.3						
400+	34.4–36.7		38.3–42.9						

TABLE 13.—*Relation of head length to standard length in Monacanthidae of the western North Atlantic, by species and millimeter intervals*

[In percent of standard length for grouped millimeter intervals of standard length]

Standard length (mm.)	Head length in percent of standard length								
	Alutera				*Monacanthus*		*Stephanolepis*		*Amanses pullus*
	monoceros	*scripta*	*schoepfii*	*heudelotii*	*tuckeri*	*ciliatus*	*hispidus*	*setifer*	
5–9.9							34.4–41.4		
10–14.9						34.5–38.2	34.3–38.3	37.5–40.2	
15–19.9			23.3		37.8–41.5	32.7–38.7	34.0–38.2	35.8–37.7	42.9
20–24.9			25.2–26.9		35.6–39.1	32.5–38.5	33.3–37.1	35.7–37.0	
25–29.9		31.5	25.3–25.5			34.4	34.4–37.3	35.7–36.3	
30–34.9		31.9–32.5	27.4–27.9	31.8–35.2	36.3–37.0	33.5–35.0	34.8–35.7	35.0–37.8	38.8
35–39.9		31.0–32.7	29.6–29.7	32.4	35.2–35.8		33.5–36.5	34.5–36.7	38.6–40.1
40–44.9		29.3	31.6–31.8	33.7–34.1	34.8	32.4–33.3	33.0–36.1	34.1–36.3	36.6–39.3
45–49.9		32.6	28.5–32.2		34.8–34.9	32.8–33.3	33.6–34.9	35.4	35.4–35.9
50–59.9	34.7	32.6–32.9	29.4–32.2	32.2	33.1–36.1	31.0–33.3	32.5–34.8	33.6–35.3	34.4–39.0
60–69.9	31.7	32.0–33.1	30.3–32.7	33.4			32.6–36.9	35.7	33.3–35.0
70–79.9	33.7	31.4–33.9	30.8–32.3	32.9–34.6		31.0–31.8	33.0–34.7	37.9	32.9–37.8
80–89.9			30.1–32.4	30.1–33.7		29.4–31.7	31.9–35.1	31.3	32.9–33.8
90–99.9		32.2	29.3–34.2			29.8–32.5	31.5–34.4	33.5–37.1	29.0–32.9
100–124.9	31.4–31.6	30.9–32.8	28.0–31.8	31.3–31.8		29.0–30.1	31.7–34.5	31.6–34.2	32.0–35.4
125–149.9	31.6	31.4–33.0	29.8–31.7	30.2–32.7			31.1–34.2		31.9–32.4
150–174.9	30.5	31.7–32.0	27.4–30.8	30.1–31.6			29.5–35.4		32.0
175–199.9			28.8–31.1	30.8–31.4			30.4–33.0		
200–224.9		32.3	27.8–29.7	29.1–30.9			29.8–31.6		
225–249.9		32.2–32.4	27.9–30.3	29.8–31.3					
250–274.9			27.8–32.2						
275–299.9			29.8						33.9
300–349.9			27.4–31.1						31.4–33.8
350–399.9		31.3	27.0–31.0						
400+	26.6–26.9		27.9–29.6						

TABLE 14.—*Relation of snout length to standard length in Monacanthidae of the western North Atlantic, by species and millimeter intervals*

[In percent of standard length for grouped millimeter intervals of standard length]

Standard length (mm.)	Snout length in percent of standard length								
	Alutera				*Monacanthus*		*Stephanolepis*		*Amanses pullus*
	monoceros	*scripta*	*schoepfii*	*heudelotii*	*tuckeri*	*ciliatus*	*hispidus*	*setifer*	
5-9.9							14.4–20.0		
10–14.9						16.4–21.0	17.5–19.3	18.4–21.0	
15–19.9			12.0		21.8–28.2	16.6–21.9	18.2–20.5	19.0–21.6	25.7
20–24.9			14.1–16.7		20.7–25.6	19.3–25.2	19.4–20.4	20.4–21.3	
25–29.9		21.9	15.8–16.6			21.4–25.1	19.6–22.3	21.2–23.2	
30–34.9		22.6–23.8	18.8–18.9	23.8–25.2	26.1–27.0	22.2–23.9	22.0–24.3	21.7–25.7	27.3
35–39.9		23.7–25.1	20.8–21.8	25.4	25.4–25.9	23.7–25.1	21.5–24.8	23.6–25.1	27.8–28.8
40–44.9		22.4	23.8–23.9	25.9–26.7	26.4	22.2–23.0	21.4–24.2	23.5–24.3	27.4–28.6
45–49.9		25.0	23.0–24.7		26.7	23.3–24.9	22.5–24.9	25.1	27.1–28.0
50–59.9	27.2	25.7–26.9	23.1–25.5	26.0	26.1–28.1	22.8–24.9	22.7–25.0	23.4–24.7	26.6–28.4
60–69.9	26.5	25.8–26.7	23.5–27.0	28.1		23.8–24.6	23.2–26.0	24.3	25.9–27.4
70–79.9	27.0	26.0–28.0	25.5–27.3	27.7–27.8		23.3–25.2	22.6–25.1	26.8	26.9–33.3
80–89.9			24.7–27.6	26.0–28.7		21.9–24.5	22.8–25.2	20.6–24.9	26.9–27.8
90–99.9		27.2	24.2–28.6			23.4–25.7	21.2–24.4	24.2–25.6	26.5–28.9
100–124.9	26.2–27.5	26.3–28.8	22.5–27.5	27.2–27.9		22.4–24.3	22.5–25.1	22.1–23.9	26.0–27.8
125–149.9	26.7	26.8–28.0	24.8–26.7	26.2–28.7			23.3–26.0		25.9–27.2
150–174.9	26.5	27.4–28.3	25.1–27.1	26.7–27.9			21.3–27.5		26.9
175–199.9			24.8–27.8	27.1–27.7			23.3–25.9		
200–224.9		28.3	23.6–27.0	26.6–28.0			22.4–24.4		
225–249.9		28.0–28.1	24.2–26.5	26.9–28.2					
250–274.9			24.2–26.9						
275–299.9			27.1						27.4
300–349.9			23.6–27.6						25.6–28.8
350–399.9		26.8	23.9–26.7						
400+	23.4–24.2		23.3–26.1						

TABLE 15.—*Relation of eye diameter to standard length in Monacanthidae of the western North Atlantic, by species and millimeter intervals*

[In percent of standard length for grouped millimeter intervals of standard length]

Standard length (mm.)	Eye diameter in percent of standard length								
	Alutera				*Monacanthus*		*Stephanolepis*		*Amanses pullus*
	monoceros	*scripta*	*schoepfii*	*heudelotii*	*tuckeri*	*ciliatus*	*hispidus*	*setifer*	
5-9.9							13.3-17.1		
10-14.9						11.8-14.5	13.3-15.7	14.0-15.9	
15-19.9			8.0		11.4-14.4	10.8-13.1	13.2-15.6	13.8-15.0	14.9
20-24.9			7.8-8.4		11.0-12.7	11.0-12.6	11.8-14.0	13.1-14.4	
25-29.9		8.5	7.2-7.8			10.9-12.8	11.3-15.8	12-4-13.9	
30-34.9		8.4-9.1	7.1-8.4	8.5-9.7	11.0-11.2	11.2-12.1	13.3-14.8	12.9-13.3	19.6
35-39.9		7.8-9.0	7.0-7.6	10.0	10.0-10.1	12.6	12.0-13.9	11.7-12.6	9.7-11.0
40-44.9		7.3	8.0-8.4	8.8-9.1	9.8	10.2-11.1	11.3-13.6	11.1-11.6	10.3-11.3
45-49.9		7.4	7.4-8.7		9.4	9.9-10.3	10.3-12.4	10.9-11.4	9.5-10.0
50-59.9	8.3	7.4-7.9	7.8-8.3	8.0	8.7-10.1	8.6-9.8	10.4-11.5	11.0-11.8	9.0-10.4
60-69.9	7.8	6.6-7.2	7.0-8.6	8.3		9.2	9.5-11.7	9.9-10.1	8.5-9.4
70-79.9	7.4	6.6-8.0	5.8-8.8	8.2-9.6		9.1-10.2	9.7-10.5	9.9-12.0	8.0-9.0
80-89.9			6.7-7.9	7.3-8.4		7.4-9.1	9.1-11.5	9.4-11.3	8.0-8.2
90-99.9		6.7	4.8-8.1			7.7-8.9	8.7-9.6	8.7-11.6	7.9-8.1
100-124.9	6.4	5.9-6.8	6.0-7.3	6.4-8.1		7.4-8.3	7.4-9.9	7.6-9.9	7.5-8.8
125-149.9	6.7	5.7-6.5	6.4-7.1	6.3-7.7			7.5-8.9		7.0-7.6
150-174.9	5.4	5.6-6.4	5.1-7.2	6.4-8.5			7.0-9.1		7.0
175-199.9			5.1-6.8	7.0-7.6			7.1-7.8		6.6
200-224.9		5.4	6.7-6.1	6.2-7.7			6.9-7.1		
225-249.9		5.5	5.3-6.1	6.6-7.5					
250-274.9			5.1-6.7						
275-299.9			5.9						5.6
300-349.9			5.0-6.4						5.2-5.3
350-399.9		5.3	4.8-6.0						
400+	4.2-4.4		4.9-5.1						

TABLE 16.—*Relation of eye to dorsal-spine distance to standard length in Monacanthidae of the western North Atlantic, by species and millimeter intervals*

[In percent of standard length for grouped millimeter intervals of standard length]

Standard length (mm.)	Eye to dorsal spine distance in percent of standard length								
	Alutera				*Monacanthus*		*Stephanolepis*		*Amanses pullus*
	monoceros	*scripta*	*schoefii*	*heudelotii*	*tuckeri*	*ciliatus*	*hispidus*	*setifer*	
5-9.9							11.7-17.1		
10-14.9						8.6-9.5	11.5-13.9	11.8-12.8	
15-19.9			4.7		9.5-10.6		11.6-12.7	12.7	7.4
20-24.9			3.9-4.8		7.7-8.8	8.8-9.8	10.8-11.4	11.1	
25-29.9		6.7	4.3-5.1			10.1	10.4-11.9	10.6-11.2	
30-34.9		5.8-6.5	4.0	4.3-7.3	7.5-7.7		9.6-11.1	9.9-13.3	7.6
35-39.9		5.1-6.4	5.1-5.5	4.9	7.0-7.2		9.7-11.0	10.3-11.5	7.5-7.9
40-44.9		6.1	4.0	4.0-5.4	7.3	9.6	8.7-11.0	9.1	7.8-9.0
45-49.9		5.7	5.1-6.7		6.5-6.7	8.0-8.4	9.5-10.5	9.3-9.9	6.9-7.9
50-59.9	8.1	6.0-6.4	5.4-7.1	7.2	6.3-7.4	8.0-9.6	8.8-10.1	8.7-10.9	6.6-8.5
60-69.9	7.8	5.4-6.1	5.4-6.8	6.6			8.9-10.5	10.9	7.1-7.7
70-79.9	7.3	5.7-6.4	6.4-6.9	5.7-6.7		8.0-9.1	8.7-10.7	9.8	7.3-8.5
80-89.9			6.7-8.1	5.7-6.7		6.7-7.9	8.8-10.7	9.4	7.2-7.9
90-99.9		6.1	6.3-8.3	6.4		7.8-8.5	8.3-10.2	8.4-10.4	8.2-8.3
100-124.9	7.8	5.8-6.0	7.3-8.9	4.6-6.6		7.0-7.9	8.4-10.6	7.7-8.6	6.6-8.3
125-149.9	8.3	5.9	7.8-8.6	5.2-6.1			7.4-10.0		5.9-6.5
150-174.9	8.6	5.1-6.0	7.7-9.2	5.1-6.1			7.4-9.8		6.6
175-199.9			8.4-11.2	4.9-5.6			8.0-8.6		
200-224.9		6.1	8.8-12.7	5.1-5.5			7.3-8.5		
225-249.9		5.0-5.5	7.5-11.0	4.8-5.3					
250-274.9			7.6-11.8						
275-299.9			8.1						8.9
300-349.9			7.9-13.5						7.4-8.3
350-399.9		5.3	7.9-12.9						
400+	7.0-7.2		12.0-13.0						

C. SPECIMENS EXAMINED

The specimens examined are listed by species and arranged generally from north to south along the Atlantic coast of the United States, including Bermuda and the Bahamas; then north, west, and south around the Gulf of Mexico; next throughout Cuba and the rest of the West Indies; and finally southward through the Caribbean and to Brazil. The few records from outside the western North Atlantic are listed terminally on the individual species lists.

The following abbreviations are used for collections:

ANSP, Academy of Natural Sciences of Philadelphia; BLBG, U.S. Fish and Wildlife Service Biological Laboratory, Brunswick, Ga.; CAS, California Academy of Sciences; CHML, Cape Haze Marine Laboratory; FSBC, Florida State Board of Conservation Marine Laboratory, St. Petersburg, Fla.; SU, Stanford University Natural History Museum; TU, Tulane University; UF, University of Florida; UNC, University of North Carolina Institute of Fisheries Research; USNM, U.S. National Museum.

The following abbreviations are used for collecting methods, in those instances in which the methods are definitely known:

D.N., dip net; M.L.N., meter larval net; P.T., plankton tow; S.C., stomach contents of a larger fish; Sn., seine; Tr., bottom trawl.

The following additional abbreviations are used: Cr., cruise; Reg., regular station; Spc., special station; Std., standard station; Sta., station; S.L., standard length.

Alutera monoceros

Woods Hole, Mass., 22 Aug. 1898, (1 specimen) 114 mm. S.L., USNM 85771.---25 miles southwest of Cuttyhunk Island, Mass., 17 Sept. 1935, (1) 144 mm. S.L., caught in lobster pot, USNM 107273.---34°05′ N., 76°21′ W., to 34°01′ N., 76°18′ W., *Albatross* Cr. 31–A, Sta. 2, tow 2, 19 Jan. 1950, (1) 520 mm. S.L., Tr. 25–75 fathoms, USNM 152089.---34°05′ N., 76°21′ W., to 34°01′ N., 76°18′ W., *Albatross* Cr. 31–A, Sta. 2, tow 2, 19 Jan. 1950, (1) 401 mm. S.L., Tr. 25–75 fathoms, USNM 152090.---Kitty Hawk, N.C., (1) 167 mm. S.L., USNM 163881.---30°34′ N., 80°17′ W., *Silver Bay* Sta. 1550, 17 Jan. 1960, (1) 545 mm. S.L., Tr. 22–21 fathoms, BLBG.---26°47′ N., 79°53′ W., *Combat* Sta. 459, 28 July 1957, (1) 122 mm. S.L., D.N., BLBG.---Tortugas, Fla., (3) 53.0–73.0 mm. S.L., collected by W. H. Longley, USNM 117022.---Port of Fortaleza, Mucuripe, Brazil, Mar. 1945, (1) 91.0 mm. S.L., SU 52309, No. 558.---Port of Fortaleza, Mucuripe, Brazil, June 1945, (1) 78.0 mm. S.L., SU 52309, No. 841.---Durban Harbor, Durban, Natal, South Africa, 8 Aug. 1933, (1) 96.5 mm. S.L., collected by H. W. B. Marley, Herre 1934 Exped., SU 31365.---China Sea, coast of Pahang, Malay Peninsula, Nov. 1926, (2) 115 and 137 mm. S.L., collection of Fisheries Dept. F. M. S., Herre 1934 Exped., SU 30786.---Manado, Indonesia, (1) 115 mm. S.L., USNM 126630.---Chame Point, Pacific Panama, (1) 49.5 mm. S.L., collected by Tweedlie, USNM 82059.

Alutera scripta

34°38′ N., 74°46′ W., *Gill* Cr. 2, Reg. 80, 12 May 1953, (1 specimen) 62.5 mm. S.L., D.N., BLBG.---34°14′ N., 76°03′ W., *Silver Bay*, 15 Sept. 1959, (3) 78.5–103 mm. S.L., D.N., BLBG.---32°34′ N., 77°48′ W., *Gill* Cr. 8, Reg. 52, 26 Sept. 1954, (1) 53.0 mm. S.L., D.N., BLBG.---Bermuda, (1) about 410 mm. S.L. (skin and skull only), collected by G. B. Goode, USNM 21889.---31°57′ N., 78°09′ W., *Gill* Cr. 3, Reg. 50, 6 Aug. 1953, (1) 39.5 mm. S.L., D.N., BLBG.---30°00′ N., 80°10′ W., *Silver Bay* Sta. 476, 18 June 1958, (1) 33.0 mm. S.L., M.L.N., BLBG.---29°40′ N., 80°00′ W., *Gill* Cr. 8, Reg. 18, 13 Sept. 1954, (1) 35.0 mm. S.L., D.N., BLBG.---29°38′ N., 80°12′ W., *Combat* Sta. 474, 14 Aug. 1957, (5) 64.0–73.0 mm. S.L., D.N., BLBG.---29°38′ N., 80°09′ W., *Silver Bay* Sta. 471, 17 June 1958, (1) 46.0 mm. S.L., M.L.N., BLBG.---29°29′ N., 80°09′ W., *Combat* Sta. 485, 18 Aug. 1957, (1) 66.0 mm. S.L., D.N., BLBG.---29°29′ N., 80°10′ W., *Combat* Sta. 490, 19 Aug. 1957, (1) 99.0 mm. S.L., D.N., BLBG.---29°10′ N., 80°19′ W., to 29°19′ N., 80°15′ W., *Combat* Sta. 336 to Sta. 337, 1 June 1957, (1) 41.0 mm. S.L., D.N., BLBG.---28°18′ N., 79°28′ W., *Gill* Cr. 8, Reg. 8, 12 Sept. 1954, (1) 39.0 mm. S.L., D.N., BLBG.---27°14′ N., 79°50′ W., *Combat* Sta. 462, 29 July 1957, (1) 53.5 mm. S.L., D.N., BLBG.---Jupiter Inlet, Fla., July 1958, (1) 27.0 mm. S.L., BLBG.---26°47′ N., 79°53′ W., *Combat* Sta. 459, 28 July 1957, (2) 119 and 128 mm. S.L., D.N., BLBG.---25°11′ N., 79°56′ W., *Combat* Sta. 443, 22 July 1957, (1) 127 mm. S.L., D.N., BLBG.---25°10′ N., 80°02′ W., *Combat* Sta. 438, 22 July 1957, (3) 31.0–121 mm. S.L., D.N., BLBG.---Tortugas, Fla., (1) 160 mm. S.L., collected by W. H. Longley, USNM 117024.---Tortugas, Fla., (2) 70.5 and 121 mm. S.L., collected by W. H. Longley, USNM 117023.---Gulf of Mexico, 30 miles southwest of Boca Grande, Fla., 21 Oct. 1956, (1) 200 mm. S.L., CHML.---Destin, Fla., about June 1958, (1) 163 mm. S.L., BLBG.---Choctawatchee Bay, Fla., June 1958, (1) 152 mm. S.L., BLBG.---28°47′ N., 87°56′ W., *Oregon* Sta. 1589, 23–24 July 1956, (2) 141 and 164 mm. S.L., USNM 158763.---29°10′ N., 88°08′ W., *Oregon* Sta. 1525, 17 May 1956, (1) 67.0 mm. S.L., TU 11639.---28°45′ N., 88°03′ W., *Oregon* Sta. 1590, 24 July 1956, (2) 164 mm. S.L., UF.---26°40′ N., 92°00′ W., *Oregon* Sta. 1035, 8 May 1954, (1) 145 mm. S.L., TU 10937.---24°50′ N., 92°35′ W., *Oregon* Sta. 2198, 23–24 June 1958, (1) 107 mm. S.L., D.N., BLBG.---20°50′ N., 86°10′ W., *Oregon* Sta. 1297, 28 Apr. 1955, (1) 35.0 mm. S.L., D.N., USNM 159168.---Cuba, 1914, (1) 244 mm. S.L., collected by Henderson and Bartsch, USNM 82569.---Cuba, (1) 57.5 mm. S.L., collected by Poey, USNM 37466.---Jamaica, (1) 230 mm. S.L., collection of Institute of Jamaica, USNM 32041.---Haiti, (1) 79.0 mm. S.L., collected by Beebe, USNM 178807.---Barbados, Antigua, (1) 377 mm. S.L., collection U. of Iowa Barbados-Antigua Exped. 1918, USNM 170118.---No data, presumably from western North Atlantic, (1) 35.5 mm. S.L., BLBG.---Chame Point, Pacific Panama, (2) 50.0–67.5 mm. S.L., USNM 82059.---Ecuador, 16 Nov. 1919, (1) 52.0 mm. S.L., USNM 84042.---No data, (1) 98.0 mm. S.L., USNM 83814.

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Halifax, Nova Scotia, (1) 95.5 mm. S.L., collected by Honeyman, USNM 22490.---Woods Hole, Mass., *Fish Hawk*, Aug. 1899, (1) 170 mm. S.L., USNM 120557.---Woods Hole, Mass., (1) 142 mm. S.L., USNM 34397.---Woods Hole, Mass., (2) 63.0 and 137 mm. S.L., USNM 119226.---Vineyard Sound, Mass., 4 Oct. 1927, (2) 118 and 132 mm. S.L., USNM 107272.---West Falmouth, Mass., 22 Aug. 1899, (1) 126 mm. S.L., USNM 120556.---Buzzards Bay, Mass., (1) 117 mm. S.L., USNM 107263.---New Bedford, Mass., (2) 96.0 and 102 mm. S.L., USFC 16542, TU 8911.---Katama Bay, Mass., 19 Aug. 1938, (1) 101 mm. S.L., USNM 107275.---Newport, R.I., (6) 131–160 mm. S.L., collected by S. Powell, USNM 20727.---Newport, R.I., (1) 143 mm. S.L., collected by S. Powell, USNM 20198.---Long Island, N.Y., (1) 163 mm. S.L., collected by Jordan, SU 1959.---Barnegat Bay, Seaside Park, N.J., July-Aug. 1926, (1) 355 mm. S.L., collected by B. A. Bean, USNM 120493.---Carson's Inlet, N.J., 9 Sept. 1916, (1) 196 mm. S.L., ANSP 46736.---Bombay Hook, Del., 10 June 1884, (1) 407 mm. S.L., Sn., USNM 34977.---Mouth of Great Wicinoco River, Chesapeake Bay, *Albatross*, (1) 355 mm. S.L., USNM 33333.---Mouth of Great Wicinoco River, Chesapeake Bay, *Albatross*, (1) 390 mm. S.L., USNM 33332.---Ocean View, Norfolk, Va., 22 Oct. 1922, (2) 116 and 130 mm. S.L., Sn., USNM 91102.---Ocean View, Va., 1-5 Oct. 1922, (4) 101–131 mm. S.L., Sn., USNM 91103.---34°58′ N., 75°54′ W., *Silver Bay* Sta. 1258, 8 Sept. 1959, (1) 367 mm. S.L., Tr. 13–14 fathoms, BLBG.---34°53.5′ N., 75°32′ W., to 34°54′ N., 75°31′ W., *Albatross III*, Cr. 31–A, Sta. 17, 22 Jan. 1950, (1) 363 mm. S.L., 23 fathoms, USNM 152092.---34°50′ N., 76°14′ W., *Silver Bay* Sta. 1254, 8 Sept. 1959, (4) 194–355 mm. S.L., Tr. 12–11 fathoms, BLBG.---34°47′ N., 76°20′ W., *Silver Bay* Sta. 1252, 8 Sept. 1959, (2) 320 and 340 mm. S.L., Tr. 9–11 fathoms, BLBG.---34°44′ N., 75°53′ W., *Silver Bay* Sta. 1271, 12 Sept. 1959, (1) 402 mm. S.L., Tr. 17 fathoms, BLBG.---34°39′ N., 76°01′ W., *Silver Bay* Sta. 1270, 12 Sept. 1959, (1) 335 mm. S.L., Tr. 20 fathoms, BLBG.---34°38′ N., 76°49′ W., *Silver Bay* Sta. 1291, 22 Sept. 1959, (1) 263 mm. S.L., Tr. 8–10 fathoms, BLBG.---34°37′ N., 77°01′ W., *Silver Bay* Sta. 1311, 24 Sept. 1959, (1) 271 mm. S.L., Tr. 7 fathoms, BLBG.---34°35′ N., 76°23′ W., *Silver Bay* Sta. 1250, 7 Sept. 1959, (1) 328 mm. S.L., Tr. 11–10 fathoms, BLBG.---34°35′ N., 77°03′ W., *Silver Bay* Sta. 1310, 24 Sept. 1959, (4) 217–260 mm. S.L., Tr. 8 fathoms, BLBG.---34°32′ N., 76°33′ W., *Silver Bay* Sta. 1317, 27 Sept. 1959, (1) 303 mm. S.L., Tr. 8 fathoms, BLBG.---34°31′ N., 76°53′ W., *Silver Bay* Sta. 1239, 6 Sept. 1959, (1) 360 mm. S.L., Tr. 14–12 fathoms, BLBG.---34°31′ N., 76°35′ W., *Silver Bay* Sta. 1242, 6 Sept. 1959, (1) 223 mm. S.L., Tr. 9 fathoms, BLBG.---Cape Lookout, N.C., July 1912, (1) 345 mm. S.L., collected by R. J. Coles, USNM 74300.---Cape Lookout, N.C., 22 Oct. 1927, (1) 72.0 mm. S.L., surface, USNM 111836.---34°29′ N., 76°57′ W., *Silver Bay* Sta. 1307, 24 Sept. 1959, (1) 360 mm. S.L., Tr. 12 fathoms, BLBG.---34°27′ N., 76°20′ W., *Silver Bay* Sta. 1249, 7 Sept. 1959, (1) 294 mm. S.L., Tr. 7 fathoms, BLBG.---34°26′ N., 77°05′ W., *Silver Bay* Sta. 1308, 24 Sept. 1959, (1) 348 mm. S.L., Tr. 9–10 fathoms, BLBG.---34°25′ N., 76°51′ W., *Silver Bay* Sta. 1294, 23 Sept. 1959, (2) 308 and 334 mm. S.L., Tr. 12–13 fathoms, BLBG.---34°23′ N., 76°54′ W., *Silver Bay* Sta. 1295, 23 Sept. 1959, (2) 309 and 352 mm. S.L., Tr. 13–15 fathoms, BLBG.---34°21′ N., 77°34′ W., *Silver Bay* Sta. 1227, 4 Sept. 1959, (2) 240 and 293 mm. S.L., Tr. 7–8 fathoms, BLBG.---34°16′ N., 77°34′ W., *Silver Bay* Sta. 1226, 4 Sept. 1959, (1) 350 mm. S.L., Tr. 8–7 fathoms, BLBG.---34°15′ N., 76°36′ W., *Silver Bay* Sta. 1236, 6 Sept. 1959, (1) 358 mm. S.L., Tr. 18 fathoms, BLBG.---34°13′ N., 76°48′ W., *Silver Bay* Sta. 1296, 23 Sept. 1959, (1) 366 mm. S.L., Tr. 17 fathoms, BLBG.---34°09′ N., 76°55′ W., *Silver Bay* Sta. 1230, 5 Sept. 1959, (2) 342 and 379 mm. S.L., Tr. 17 fathoms, BLBG.---34°09′ N., 76°35′ W., *Silver Bay* Sta. 1297, 23 Sept. 1959, (2) 243 and 251 mm. S.L., Tr. 20 fathoms, BLBG.---34°07′ N., 77°19′ W., *Silver Bay* Sta. 1224, 4 Sept. 1959, (1) 372 mm. S.L., Tr. 13 fathoms, BLBG.---33°56′ N., 77°20′ W., *Silver Bay* Sta. 1215, 3 Sept. 1959, (4) 330–372 mm. S.L., Tr. 15 fathoms, BLBG.---33°47′ N., 77°50′ W., *Silver Bay* Sta. 1210, 2 Sept. 1959, (2) 136 and 355 mm. S.L., Tr. 8 fathoms, BLBG.---33°45′ N., 76°50′ W., *Silver Bay* Sta. 1218, 3 Sept. 1959, (6) 374–410 mm. S.L., Tr. 23–24 fathoms, BLBG.---33°41′ N., 77°40′ W., *Silver Bay* Sta. 1209, 2 Sept. 1959, (2) 309–332 mm. S.L., Tr. 11–12 fathoms, BLBG.---33°32′ N., 77°30′ W., *Silver Bay* Sta. 1208, 2 Sept. 1959, (3) 300–358 mm. S.L., Tr. 14 fathoms, BLBG.---32°54′ N., 77°04′ W., *Gill* Cr. 3, Reg. 61, 10 Aug. 1953, (1) 20.5 mm. S.L., D.N., BLBG.---32°24′ N., 78°45′ W., *Gill* Cr. 8, Reg. 48, 25 Sept. 1954, (1) 23.0 mm. S.L., D.N., BLBG.---Charleston, S.C., (1) 124 mm. S.L., collected by J. C. Mitchell, USNM 30727.---Bermuda, (1) 365 mm. S.L., USNM 23859.---31°00′ N., 80°23′ W., *Gill* Cr. 4, Reg. 32, 16 Oct. 1953, (1) 26.5 mm. S.L., D.N., BLBG.---Commercial Trawling Area, Brunswick, Ga., 9–13 Apr. 1956, (1) 187 mm. S.L., Tr., BLBG.---Commercial Trawling Area, Brunswick, Ga., 23 Sept. 1956, (1) 96.0 mm. S.L., Tr., BLBG.---30°20′ N., 80°36′ W., *Gill* Cr. 7, Reg. 25, 26 June 1959, (1) 22.5 mm. S.L., D.N., BLBG.---29°32′ N., 80°25′ W., *Combat* Sta. 348, 2 June 1957, (1) 355 mm. S.L., Tr. 22 fathoms, BLBG.---Port Canaveral Anchorage, Fla., *Combat*, 28–29 Apr. 1957, (1) 32.5 mm. S.L., D.N., BLBG.---Jupiter Inlet, Fla., Sept.–Nov. 1958, (3) 22.7–33.0 mm. S.L., UF.---Jupiter Inlet, Fla., Aug. 1958, (1) 68.0 mm. S.L., UF.---Jupiter Inlet, Fla., June 1958, (1) 377 mm. S.L., UF.---27°04′ N., 80°04′ W., *Gill* Cr. 2, Reg. 5, 23 Apr. 1953, (1) 15.0 mm. S.L., D.N., BLBG.---Biscayne Bay, Fla., *Launch 58*, 5 Sept. 1938, (1) 126 mm. S.L., Tr., USNM 155986.---Tortugas, Fla., (5) 27.5–62.5 mm. S.L., collected by W. H. Longley, USNM 117026.---Cape Haze, Fla., 2 July 1958, (1) 49.0 mm. S.L., CHML.---Gasparilla Bay, Fla., (1) 337 mm. S.L., CHML.----Gasparilla Bay, Fla., (1) 233 mm. S.L., CHML.----Gasparilla Sound, Placida, Fla., 10 May 1955, (1) 197 mm. S.L., CHML.----Gasparilla Sound, Placida, Fla., 9 Apr. 1956, (1) 187 mm. S.L., CHML.----Gasparilla Sound, Placida, Fla., 26 May 1958, (1) 250 mm. S.L., TU 18493.----Lemon Bay, Fla., 28 Sept. 1955, (1) 98.0 mm. S.L., CHML.----Lemon Bay, Fla., summer 1956, (1) 95.0 mm. S.L., CHML.----Lemon Bay, Fla., May 1957, (1) 41.0 mm. S.L., CHML.----Englewood Beach, Fla., 26 Aug. 1956, (1) 30.0 mm. S.L., CHML.----Pass-a-Grille to Venice, Fla., 10–11 Feb. 1958, (1) 306 mm. S.L., FSBC VGS 58–41.----Egmont Key, Fla., 23 Mar. 1958, (12) 218–257 mm. S.L., TU 17941.----Mullet Key, Boca Ciega Bay, Fla., 4 June 1958, (1) 64.0 mm. S.L., FSBC VGS 58–152.----Bird Key, Boca Ciega Bay, Fla., 7 July 1958, (2) 89.0 and 95.0 mm. S.L., FSBC VGS 58–181.----Bird Key, Boca Ciega Bay, Fla., 7 July 1958, (1) 273 mm. S.L., FSBC VGS 58–276.----City dock, Clearwater, Fla., 5 Aug. 1948, (1) 96.0 mm. S.L., pole-and-line, USNM.----Cedar Keys, Fla., 18–20 Aug. 1949, (2) 62.5 and 93.5 mm. S.L., UF.----Cedar Keys, Fla., 7 Nov. 1950, (1) 73.0 mm. S.L., UF.----Piney Point, Cedar Keys, Fla., 7 June 1950, (2) 37.0–38.5 mm. S.L. UF.----Cedar Keys, Fla., 3 Oct. 1953, (1) 190 mm. S.L., UF C–10–353–4.----Cedar Keys, Fla., 20 Sept. 1953, (2) 158 and 176 mm. S.L., UF C–9–2053–3.----Cedar Keys, Fla., 20 Sept. 1953, (1) 159 mm. S.L., UF.----Cedar Keys, Fla., 6 Sept. 1953, (1) 126 mm. S.L., UF 2542.----Cedar Keys, Fla., 16 Aug. 1953, (1) 103 mm. S.L., UF C–8–1653–5.----Cedar Keys, Fla., 25 July 1953, (3) 60.0–96.0 mm. S.L., UF C–7–2553–4.----Cedar Keys, Fla., 12 July 1953, (1) 98.0 mm. S.L., UF C–7–1253–5.----Cedar Keys, Fla., 12 July 1953, (1) 80.5 mm. S.L., UF C–7–1253–1.----Cedar Keys, Fla., 12 July 1953, (1) 118 mm. S.L., UF C–7–1253–4.----Cedar Keys, Fla., 12 July 1953, (2) 91.0 and 165 mm. S.L., UF C–7–1253–7.----Cedar Keys, Fla., 12 July 1953, (1) 68.0 mm. S.L., UF 2475.----Cedar Keys, Fla., 1 July 1953, (1) 64.0 mm. S.L., UF 2457.----Cedar Keys, Fla., 28 June 1953, (4) 47.0–81.5 mm. S.L., UF C–6–2853–3.----Cedar Keys, Fla., 28 June 1953, (1) 59.0 mm. S.L., UF C–6–2853–1.----Cedar Keys, Fla., 30 June 1954, (1) 85.5 mm. S.L., UF C–6–3054–6.----Cedar Keys, Fla., 15–16 Aug. 1955, (3) 47.0–72.5 mm. S.L., TU 11953.----Cedar Keys, Fla., 11–13 June 1957, (39) 46.5–73.0 mm. S.L., USNM 176239.----Cedar Keys, Fla., 23 Nov. 1957, (1) 86.5 mm. S.L., UF.----Destin, Fla., Nov. 1956, (1) 213 mm. S.L., UF.----Fort Walton Beach, Fla., Nov. 1956, (1) 325 mm. S.L., UF.----Pensacola, Fla., (1) 185 mm. S.L., CAS C87 3519.----Florida, *Orian*, (1) 126 mm. S.L., collected by B. A. Bean and J. A. Pine, USNM 62555.----28°47′ N., 87°56′ W., *Oregon* Sta. 1589, 23–24 July 1956, (1) 68.5 mm. S.L., D.N., USNM 158763.----28°44′ N., 88°08′ W., *Oregon* Sta. 1583, 20–21 July 1956, (1) 59.0 mm. S.L., D.N., UF.----29°22′ N., 88°48′ W., *Oregon* Sta. 1109, 15 June 1954, (5) 317–343 mm. S.L., TU 17106.----Mississippi coast, (1) 124 mm. S.L., USNM 147796.----Grand Isle, La., (1) 119 mm. S.L., USNM 125803.----Oyster Bayou, Terrebonne County, La., June–July 1954, (1) 60.5 mm. S.L., TU 9039.----Freeport, Tex., Jan.–May 1947, (1) 309 mm. S.L., USNM 147808.----Aransas Pass, Tex., 11 Oct. 1926, (1) 35.8 mm. S.L., USNM 156000.----Aransas Pass, Tex., 5–7 June 1954, (4) 32.3–51.3 mm. S.L., TU 11781.----Harbor Island, Corpus Christi, Tex., 5 Oct. 1926, (2) 74.5 and 78.0 mm. S.L., USNM 156002.----Corpus Christi, Tex., (1) 72.0 mm. S.L., USNM 94553.----Corpus Christi, Tex., (1) 140 mm. S.L., USNM 94554.----Hahia Honda, Cuba, 5 June 1914, (1) 272 mm. S.L., collected by Henderson and Bartsch, USNM 82568.----Hahia Honda, Cuba, 5 June 1914, (1) 283 mm. S.L., collected by Henderson and Bartsch, USNM 82567.----Kingston, Jamaica, (1) 290 mm. S.L., SU 11808.----Jamaica, B.W.I., (3) 105–170 mm. S.L., collected by J. S. Roberts, SU 4880.----Jamaica, (1) 134 mm. S.L., collected by Adams, USNM 4910.----Bizoton Wharf, Haiti, (1) 65.0 mm. S.L., collected by Beebe, USNM 178063.----Bizoton, Haiti, (10) 25.0–53.5 mm. S.L., collected by Beebe, USNM 178917.---- Haiti, (1) 92.5 mm. S.L., collected by Beebe, USNM 178055.----Off Nicaragua, *Oregon*, (1) 237 mm. S.L., USNM 159204.----Chiriqui Lagoon, Atlantic Panama, 12 July 1933, (1) 37.5 mm. S.L., USNM 178916.----Fox Bay, Colon, Atlantic Panama, 5 Jan. 1911, (2) 91.5 and 115 mm. S.L., USNM 81516.----Colon, Panama, summer 1916, (1) 132 mm. S.L., ANSP 49071.----Brazil, *Albatross*, (1) 67.5 mm. S.L., USNM 43291.----No data, presumably from western North Atlantic, (1) 328 mm. S.L., BLBG.----No data, presumably from western North Atlantic, (1) 44.0 mm. S.L., BLBG.----No data, (1) 184 mm. S.L., USNM 91471.----No data, (2) 120 and 121 mm. S.L., USNM 91472.----No data, (1) 130 mm. S.L., USNM 91469.----No data, (1) 151 mm. S.L., USNM 91470.

Alutera heudelotii

Off southern Massachusetts, Nov. 1949, (1) 158 mm. S.L., USNM 148340.—North Carolina coast, *Albatross III* Cr. 31–B, Jan.–Feb. 1950, (1) 240 mm. S.L., USNM 152043.----84°45′20′′ N., 75°38′10′′ W., *Albatross* Sta. 2599, 18 Oct. 1885, (1) 29.2 mm. S.L., USNM 131492.----34°45′ N., 75°38′ W., *Combat* Sta. 386, 17 June 1957, (1) 125 mm. S.L., Tr. 45 fathoms, BLBG.----34°39′ N., 76°01′ W., *Silver Bay* Sta. 1270, 12 Sept. 1959, (3) 140–172 mm. S.L., Tr. 20 fathoms, BLBG.----34°38′30′′ N., 75°33′30′′ W., *Albatross* Sta. 2603, 18 Oct. 1885, (1) 27.0 mm. S.L., USNM 131596.----34°05′ N., 76°21′ W., to 34°01′ N., 76°18′ W., *Albatross III* Cr. 31–A, tow 2, (1) 220 mm. S.L., Tr. 25–75 fathoms, USNM 152091.----33°29′ N., 77°22′ W., *Silver Bay* Sta. 1205, 1 Sept. 1959, (1) 232 mm. S.L., Tr. 16–20 fathoms, BLBG.----33°21′ N., 77°24′ W., *Silver Bay* Sta. 1204, 1 Sept. 1959, (1) 171 mm. S.L., Tr. 15–16 fathoms, BLBG.----Bermuda, (1) 69.5 mm. S.L., collected by Beebe, USNM.----Miami, Fla., 24 Oct. 1953, (1) 78.0 mm. S.L., CHML.----25°10′ N., 80°02′ W., *Combat* Sta. 438, 22 July 1957, (6) 31.0–108 mm. S.L., D.N., BLBG.----24°13′ N., 81°42′ W., *Combat* Sta. 436, 21 July 1957, (1) 69.5 mm. S.L., BLBG.----Tortugas, Fla., (2) 71.5 and 92.5 mm. S.L., collected by W. H. Longley, USNM 117025.----Tortugas, Fla., (4) 42.5–54.0 mm. S.L., collected by W. H. Longley, USNM 88106.----Channel west of White Shoal, Tortugas, Fla., 22 June 1932, (1) 78.5 mm. S.L., USNM 109177 (lectotype).----Channel west of White Shoal, Tortugas, Fla., 22 June 1932, (5) 48.5–63.5 mm. S.L., USNM 109178, (paratypes).---Tortugas, Fla., (7) 29.7–69.5 mm. S.L., collected by W. H. Longley, USNM 117027.---Tortugas, Fla., mid-April 1956, (1) 165 mm. S.L., CHML.---Tortugas, Fla., June–Aug. 1926, (1) 60.0 mm. S.L., USNM 88105.---26°11′ N., 82°48′ W., *Oregon* Sta. 987, 7 Apr. 1954, (1) 121 mm. S.L., Tr. 20 fathoms, UF 3880.---28°23′ N., 84°49′ W., *Oregon* Sta. 916, 10 Mar. 1954, (1) 131 mm. S.L., Tr. 37 fathoms, UF 3603.---28°22′ N., 84°53′ W., *Oregon* Sta. 917, 10 Mar. 1954, (3) 131–136 mm. S.L., Tr. 48 fathoms, TU 13180.---29°07′ N., 84°54′ W., *Oregon* Sta. 890, 7 Mar. 1954, (1) 206 mm. S.L., Tr. 19 fathoms, UF 3588.---29°00′ N., 85°02′ W., *Oregon* Sta. 891, 7 Mar. 1954, (1) 173 mm. S.L., Tr. 21 fathoms, UF 3648.---29°36′ N., 86°01′ W., *Silver Bay* Sta. 159, 23 Aug. 1957, (2) 136 and 198 mm. S.L., Tr., USNM.---28°47′ N., 87°56′ W., *Oregon* Sta. 1589, 23–24 July 1956, (1) 40.0 mm. S.L., USNM 158763.---27°55′ N., 88°05′ W., *Oregon* Sta. 1139, 24 July 1954, (1) 50.0 mm. S.L., TU 13164.---29°20′ N., 88°20′ W., *Silver Bay* Sta. 14, 1 July 1957, (1) 230 mm. S.L., TU 16316.---27°35′ N., 89°35′ W., *Oregon* Sta. 1133, 22 July 1954, (1) 33.0 mm. S.L., TU 13032.---28°10′ N., 94°05′ W., *Silver Bay* Sta. 9, 29 June 1957, (1) 211 mm. S.L., TU 16270.---28°12′ N., 94°10′ W., *Silver Bay* Sta. 8, 29 June 1957, (1) 220 mm. S.L., TU 16256.---28°28′ N., 94°20′ W., *Silver Bay* Sta. 6, 25 June 1957, (1) 204 mm. S.L., TU 16230.---28°02′ N., 94°39′ W., *Oregon* Sta. 143, 21 Nov. 1950, (1) 102 mm. S.L., TU 2021.---24°00′ N., 96°50′ W., *Oregon* Sta. 1074, 25 May 1954, (1) 30.5 mm. S.L., D.N., UF 3829.---18°43′ N., 93°30′ W., *Oregon* Sta. 1060, 16 May 1954, (1) 81.0 mm. S.L., UF.---24°50′ N., 92°35′ W., *Oregon* Sta. 2198, 23–24 June 1958, (5) 31.5–43.0 mm. S.L., D.N., BLBG.---Ambergris Cay, Yucatan, (1) 136 mm. S.L., USNM 79247.---Recife, Brazil, (2) 188 and 195 mm. S.L., SU 52306.

Monacanthus ciliatus

Off Georges Bank, Mass., *Caryn*, (1 specimen) 30.3 mm. S.L., BLBG.---35°08′ N., 75°22′ W., *Gill* Cr. 8, Reg. 78, 29 Sept. 1954, (1) 18.0 mm. S.L., D.N., BLBG.---34°32′ N., 75°53′ W., *Silver Bay* Sta. 1268, 11 Sept. 1959, (1) 77.5 mm. S.L., Tr. 31–30 fathoms, BLBG.---34°10′ N., 77°30′ W., *Gill* Cr. 8, Reg. 67, 28 Sept. 1954, (1) 16.2 mm. S.L., D.N., BLBG.---34°04′ N., 76°14′ W., *Gill* Cr. 7, Reg. 71, 10 July 1954, (1) 23.8 mm. S.L., D.N., BLBG.---33°45′ N., 76°50′ W., *Silver Bay* Sta. 1218, 3 Sept. 1959, (7) 43.0–85.5 mm. S.L., Tr. 23–24 fathoms, BLBG.---33°32′ N., 77°30′ W., *Silver Bay* Sta. 1208, 2 Sept. 1959, (4) 41.6–51.1 mm. S.L., Tr. 14 fathoms, BLBG.---33°29′ N., 77°22′ W., *Silver Bay* Sta. 1205, 1 Sept. 1959, (2) 72.5 and 77.0 mm. S.L., Tr. 16–20 fathoms, BLBG.---33°29′ N., 76°40′ W., *Gill* Cr. 3, Reg. 64, 11 Aug. 1953, (3) 21.0–21.5 mm. S.L., D.N., BLBG.---33°17′ N., 78°38′ W., *Gill* Cr. 8, Reg. 55, 26 Sept. 1954, (15) 15.5–21.5 mm. S.L., D.N., BLBG.---33°03′ N., 78°21′ W., *Gill* Cr. 7, Reg. 54, 4 July 1954, (1) 15.3 mm. S.L., D.N., BLBG.---33°03′ N., 78°21′ W., *Gill* Cr. 8, Reg. 54, 26 Sept. 1954, (1) 24.6 mm. S.L., D.N., BLBG.---32°56′ N., 78°06′ W., *Combat* Sta. 283, 19 Apr. 1957, (1) 101 mm. S.L., Tr. 50 fathoms, BLBG.---32°54′ N., 77°04′ W., *Gill* Cr. 3, Reg. 61, 10 Aug. 1953, (2) 21.7 and 21.8 mm. S.L., D.N., BLBG.---32°50′ N., 77°27′ W., *Combat* Sta. 295, 21 Apr. 1957, (2) 23.9 and 25.8 mm. S.L., D.N., BLBG.---32°24′ N., 78°45′ W., *Gill* Cr. 8, Reg. 48, 25 Sept. 1954, (1) 18.5 mm. S.L., D.N., BLBG.---Bermuda, (1) 51.0 mm. S.L., collected by J. M. Jones, USNM 21249.---Bermuda, (1) 51.0 mm. S.L., collected by Beebe, USNM 178766.---Castle Roads, Bermuda, 11–12 Sept. 1931, (6) 23.7–43.0 mm. S.L., dredge 12–20 ft., USNM 178785.---Nonsuch, Bermuda, (6) 39.5–52.0 mm. S.L., collected by Beebe, USNM 178862.---Nonsuch, Bermuda, 18 Oct. 1930, (4) 35.5–43.5 mm. S.L., USNM 178859.---31°00′ N., 80°23′ W., *Gill* Cr. 4, Reg. 32, 16 Oct. 1953, (2) 19.0–24.0 mm. S.L., D.N., BLBG.---30°00′ N., 80°10′ W., *Silver Bay* Sta. 476, 18 June 1958, (26) 11.0–21.9 mm. S.L., M.L.N., BLBG.---29°48′ N., 80°12′ W., *Silver Bay* Sta. 470, 17 June 1958, (14) 15.7–19.5 mm. S.L., D.N., BLBG.---29°38′ N., 80°09′ W., *Silver Bay* Sta. 471, 17 June 1958, (25) 12.4–20.1 mm. S.L., M.L.N., BLBG.---29°29′ N., 80°09′ W., *Combat* Sta. 485, 18 Aug. 1957, (4) 14.0–18.7 mm. S.L., D.N., BLBG.---29°26′ N., 80°08′ W., *Combat* Sta. 315, 27 Apr. 1957, (2) 16.5–16.8 mm. S.L., D.N., BLBG.---29°19′ N., 80°18′ W., *Combat* Sta. 339, 1 June 1957, (1) 109 mm. S.L., Tr. 25 fathoms, BLBG.---29°10′ N., 80°19′ W., *Combat* Sta. 336, 1 June 1957, (1) 21.2 mm. S.L., D.N., BLBG.---29°00′ N., 79°26′ W., *Gill* Cr. 4, Reg. 16, 14 Oct. 1953, (1) 24.3 mm. S.L., D.N., BLBG.---28°58′ N., 80°13′ W., *Combat* Sta. 333, 1 June 1957, (1) 107 mm. S.L., Tr. 30 fathoms, BLBG.---28°19′ N., 79°26′ W., *Gill* Cr. 3, Reg. 8, 26 July 1953, (2) 18.0 and 20.5 mm. S.L., D.N., BLBG.---28°15′ N., 77°01′ W., *Gill* Cr. 9, Spc. 6–7, 5 Nov. 1954, (1) about 23 mm. S.L., S.C. of *Thunnus albacares* (Bonnaterre) BLBG.---28°09′ N., 79°21′ W., *Gill* Cr. 7, Spc. 9 to Reg. 8, 24 June 1954, (1) S.C. of *Thunnus atlanticus* (Lesson), BLBG.---27°36′ N., 83°40′ W., *Oregon* Sta. 935, 18 Mar. 1954, (1) 111 mm. S.L., Tr. 27 fathoms, UF 3665.---27°34′ N., 80°04′ W., *Gill* Cr. 7, Reg. 4–5, 23 June 1954, (1) 15.5 mm. S.L., S.C. of *Euthynnus alletteratus* (Rafinesque) BLBG.---27°14′ N., 79°50′ W., *Combat* Sta. 462, 29 July 1957, (1) 22.0 mm. S.L., D.N., BLBG.---27°01′ N., 80°04′ W., *Gill* Cr. 2, Reg. 3, 23 Apr. 1953, (3) 15.3–19.9 mm. S.L., D.N., BLBG.---Settlement Point, Grand Bahama Island, *Gill* Cr. 8, 29 Aug. 1954, (15) 13.6–21.5 mm. S.L., D.N., BLBG.---26°47′ N., 79°53′ W., *Combat* Sta. 459, 28 July 1957, (3) 23.0–25.0 mm. S.L., D.N., BLBG.---26°45′ N., 78°55′ W., *Gill* Cr. 4, 3 Oct 1955, 1600, (1) about 15 mm. S.L., S.C. of *Thunnus atlanticus*, BLBG.---26°45′ N., 78°55′ W., *Gill* Cr. 4, 3 Oct. 1955, 1555, (2) about 17 mm. S.L., S.C. of *Thunnus atlanticus*, BLBG.---Hawks Bill Creek, Grand Bahama Island, *Gill* Cr. 4, 3 Oct. 1953, 1900–2100, (6) 12.8–22.7 mm. S.L., D.N., BLBG.---Hawks Bill Creek, Grand Bahama Island, *Gill* Cr. 4, 3 Oct. 1953, 2130–2330, (1) 21.8 mm. S.L., D.N., BLBG.---26°09′ N., 78°12′ W., *Gill* Cr. 7, 22 June 1954, (1) 16.5 mm. S.L., S.C. of *Thunnus atlanticus*, BLBG.---26°05′ N., 78°12′ W., *Gill* Cr. 4, Nassau to Reg. 1, 11 Oct. 1953, (6) about 12–18 mm. S.L., S.C. of *Sphyraena barracuda* (Walbaum), BLBG.---Hatchet Bay, Eleuthera Island, Bahamas, (1) 93.5 mm. S.L., UF 3504.---25°16′ N., 80°07′ W., *Combat* Sta. 457, 26 July 1957, (11) 14.8–20.7

mm. S.L., D.N., BLBG.___25°13′ N., 80°10′ W., *Combat* Sta. 455, 26 July 1957, (5) 16.0–18.7 mm. S.L., D.N., BLBG.___25°13′ N., 80°10′ W., *Combat* Sta. 455, 26 July 1957, (1) 39.0 mm. S.L., D.N., BLBG.___25°10′ N., 80°02′ W., *Combat* Sta. 438, 22 July 1957, (7) 16.5–29.5 mm. S.L., D.N., BLBG.___24°04′ N., 79°15′ W., *Combat* Sta. 448, 24 July 1957, (1) 13.5 mm. S.L., D.N., BLBG.___Key West, Fla., (11) 39.0–58.0 mm. S.L., collected by D. S. Jordan, SU 2358.___Pulaski Light, near Tortugas, Fla., (1) 100 mm. S.L., UF.___Tortugas, Fla., Apr. 1956, (2) 95.0–102 mm. S.L., CHML.___West of Loggerhead Key, Fla., (4) 75.5–87.0 mm. S.L., UF.___Sanibel Island, Fla., 14 Aug. 1959, (10) 27.6–51.5 mm. S.L., BLBG.___Sanibel Island, Fla., 19 Aug. 1959, (4) 47.5–58.0 mm. S.L., BLBG.___Cedar Keys, Fla., Sept.–Oct. 1948, (18) 17.3–69.5 mm. S.L., UF 730.___Cedar Keys, Fla., 8–9 Oct. 1948, (1) 34.4 mm. S.L., UF.___Cedar Keys, Fla., 16 Aug. 1953, (18) 25.4–54.7 mm. S.L., UF C–8–1653–4.___Cedar Keys, Fla., 6 Sept. 1953, (1) 41.6 mm. S.L., UF C–9–653–4.___Cedar Keys, Fla., 20 Sept. 1953, (1) 54.0 mm.. S.L., UF C–9–2053–3.___Cedar Keys, Fla., 1 Nov. 1953, (3) 21.1–57.0 mm. S.L., UF C–11–153–2.___Cedar Keys, Fla., 13 Nov. 1953, (1) 57.5 mm. S.L., UF C–11–1353–6.___Cedar Keys, Fla., 30 June 1954, (1) 40.6 mm. S.L., UF C–6–3054–5.___Cedar Keys, Fla., (17) 30.9–51.3 mm. S.L., UF.___27°30′ N., 84°14′ W., *Oregon* Sta. 937, 18 Mar. 1954, (4) 92.5–103 mm. S.L., Tr. 38 fathoms, UF 3611.___22°13′ N., 89°43′ W., *Silver Bay* Sta. 404, 12 May 1958, (1) 92.5 mm. S.L., Tr. 25 fathoms, USNM.___22°23′ N., 89°44′ W., *Oregon* Sta. 2174, 11–12 May 1958, (30) 12.7–21.8 mm. S.L., D.N., USNM.___24°50′ N., 92°35′ W., *Oregon* Sta. 2198, 23–24 June 1958, (1) 23.3 mm. S.L., D.N., BLBG.___Jamaica, (3) 66.0–85.0 mm. S.L., collected by J. S. Roberts, SU 4857.___Bizoton, Haiti, 3 Feb. 1927, (1) 42.0 mm. S.L., Sn., USNM 178538.___St. Thomas, Virgin Islands, (1) 45.0 mm. S.L., collected by Beebe, USNM 178812.___Pointe-a-Pitre, Guadaloupe, May 1946, (1) 33.5 mm. S.L., USNM 132624.___English Harbor, Antigua, Leeward Islands, (1) 61.0 mm. S.L., USNM 170300.___Martinique, West Indies, 17 Apr. 1937, (1) 50.0 mm. S.L., collection of Smithsonian Institute Hartford Exped., USNM 117429.___Union Island, Grenadines, (1) 19.5 mm. S.L., collected by Beebe, USNM 169962.___15°57′ N., 82°06′ W., *Oregon* Sta. 1935, 15 Sept. 1957, (1) 72.0 mm. S.L., USNM 185267.___07°55′ N., 57°27′ W., *Oregon* Sta. 2247, 31 Aug. 1958, (4) 70.5–77.5 mm. S.L., Tr. 44–37 fathoms, BLBG.___(23) 36.3–71.6 mm. S.L., SU 1958.___No data, presumably from western North Atlantic, (2) 61.0 and 80.0 mm. S.L., BLBG.

Monacanthus tuckeri

Castle Roads, Bermuda, 11–12 Sept. 1931, (7) 25.0–43.0 mm. S.L., dredge 12–20 ft., USNM 178785.___33°29′ N., 76°40′ W., *Gill* Cr. 3, Reg. 64, 11 Aug. 1953, (1) 21.4 mm. S.L., D.N., BLBG.___Nonsuch, Bermuda, 18 Oct. 1930, (3) 30.5–51.0 mm. S.L., USNM 178859.___Nonsuch, Bermuda, (1) 55.5 mm. S.L., collected by Beebe, USNM 178862.___Bermuda, (2) 36.0 and 43.0 mm. S.L., collected by J. M. Jones, USNM 21249.___29°38′ N., 80°09′ W., *Silver Bay* Sta. 471, 17 June 1958, (1) 17.0 mm. S.L., M.L.N., BLBG.___Settlement Point, Grand Bahama Island, *Gill* Cr. 8, 29 Aug. 1954, (5) 17.4–23.0 mm. S.L., D.N., BLBG.___26°45′ N., 78°55′ W., *Gill* Cr. 4, 3 Oct. 1953, 1600, (1) about 20 mm. S.L., S.C. of *Thunnus atlanticus* (Lesson), BLBG.___Hawks Bill Creek, Grand Bahama Island, *Gill* Cr. 4, 3 Oct. 1953, 1900–2100, (2) 17.9 and 18.7 mm. S.L., D.N., BLBG.___Hawks Bill Creek, Grand Bahama Island, *Gill* Cr. 4, 3 Oct. 1953, 2130–2330, (4) 16.7–20.3 mm. S.L., D.N., BLBG.___26°30′ N., 78°40′ W., *Gill* Cr. 4, 3 Oct. 1953, 1730, (1) about 18 mm. S.L., S.C. of *Thunnus atlanticus*, BLBG.___25°56.5′ N., 77°54′ W., *Gill* Cr. 7, 22 June 1954, (1) about 20 mm. S.L., S.C. of *Katsuwonus pelamis* (Linnaeus), BLBG.___25°20′ N., 77°15′ W., *Gill* Cr. 6, 19 Apr. 1954, (1) 21.0 mm. S.L., S.C. of *Coryphaena hippurus* Linnaeus, BLBG.___Nassau Harbor, Bahamas, 20 Apr. 1958, (3) 15.3–17.2 mm. S.L., ANSP 84471.___New Providence, Hog Island, Bahamas, 22 Mar. 1952, (2) 51.5 and 53.0 mm. S.L., ANSP 72669.___Hog Island, Bahamas, 25 Apr. to 3 May 1957, (3) 16.0–24.0 mm. S.L., ANSP 84482.___Periwinkle Rock, Rose Island, Bahamas, 4 Aug. 1955, (3) 49.0–56.5 mm. S.L., ANSP 84478.___Rose Island, Bahamas, 31 July 1955, (13) 20.8–50.5 mm. S.L., ANSP 84481.___Andros Island, Bahamas, (1) 18.7 mm. S.L., collected by P. Cloud, USNM 174977.___Antigua, Leeward Islands, 20 Apr. 1958, (1) 22.5 mm. S.L., dredge, USNM 183569.___St. Croix, Virgin Islands, West Indies, (4) 20.3–23.3 mm. S.L., CAS 12403.

Stephanolepis hispidus

Georges Bank, *Caryn*, (19) 13.8–46.5 mm. S.L., collected by B. B. Leavitt, BLBG.___Newport, R.I., (1) 111 mm. S.L., collected by S. Powell, USNM 21631.___36°30′ N., 74°33′ W., *Albatross*, (2) 22.5 and 33.0 mm. S.L., USNM 38330.___34°58′ N., 75°54′ W., *Silver Bay* Sta. 1258, 8 Sept. 1959, (1) 86.3 mm. S.L., Tr. 13–14 fathoms, BLBG.___34°56′ N., 75°56′ W., *Silver Bay* Sta. 1257, 8 Sept. 1959, (3) 82.5–173 mm. S.L., Tr. 13–14 fathoms, BLBG.___34°45′ N., 75°38′ W., *Combat* Sta. 386, 17 June 1957, (1) 137 mm. S.L., Tr. 40 fathoms, BLBG.___34°44′ N., 75°53′ W., *Silver Bay* Sta. 1271, 12 Sept. 1959, (1) 59.6 mm. S.L., Tr. 17 fathoms, BLBG.___Beaufort Inlet, N.C., 17 July 1954, (1) 67.5 mm. S.L., UNC 2237.___Beaufort Inlet to Cape Lookout, N.C., Sept. 1956, (5) 79.0–93.5 mm. S.L., UNC 889.___Newport River Narrows, Carteret County, N.C., 8 July 1955, (11) 58.0–74.5 mm. S.L., UNC 210.___Piver's Island, N.C., 8 July 1959, (64) 24.0–44.0 mm. S.L., Sn., BLBG.___Piver's Island, N.C., 8 July 1959, (6) 28.3–38.2 mm. S.L., Sn., BLBG.___Piver's Island, N.C., 10 July 1959, (135) 13.5–48.0 mm. S.L., Sn., BLBG.___Piver's Island, N.C., 10 July 1959, (2) 43.9 and 47.1 mm. S.L., Sn., BLBG.___Piver's Island, N.C., 4 Aug. 1954, (1) 100 mm. S.L., UNC 2545.___Morehead City, N.C., 13 July 1959, (4) 37.0–46.5 mm. S.L., Sn., BLBG.___Morehead City, N.C., 10 July 1959, (3) 30.0–40.0 mm. S.L., BLBG.___Bogue Sound, Carteret County, N.C., 29 July 1958, (2) 38.3 and 94.5 mm. S.L., UNC 2363.___34°41′ N., 76°50′ W., *Silver Bay* Sta. 1288, 20 Sept. 1959, (1) 90.8 mm. S.L., Tr. 7–5 fathoms, BLBG.___34°39′ N., 76°01′ W., *Silver Bay* Sta. 1270, 12 Sept. 1959, (4) 104–108 mm. S.L., Tr. 20 fathoms, BLBG.---34°39′ N., 76°27′ W., *Silver Bay* Sta. 1262, 10 Sept. 1959, (1) 92.3 mm. S.L., Tr. 6–7 fathoms, BLBG.---34°38′ N., 76°49′ W., *Silver Bay* Sta. 1291, 22 Sept. 1959, (5) 83.1–98.3 mm. S.L., Tr. 8–10 fathoms, BLBG.---34°38′ N., 76°40′ W., *Silver Bay* Sta. 1284, 20 Sept. 1959, (1) 87.0 mm. S.L., Tr. 6–8 fathoms, BLBG.---34°38′ N., 76°40′ W., *Silver Bay* Sta. 1284, 20 Sept. 1959, (3) 79.3–113 mm. S.L., Tr. 6–8 fathoms, BLBG.---34°38′ N., 76°49′ W., *Silver Bay* Sta. 1240, 6 Sept. 1959, (3) 87.6–97.6 mm. S.L., Tr. 7 fathoms, BLBG.---34°37′ N., 77°01′ W., *Silver Bay* Sta. 1311, 24 Sept. 1959, (2) 110 and 124 mm. S.L., Tr. 7 fathoms, BLBG.---34°35′ N., 75°15′ W., *Gill* Cr. 7, 13 July 1954, (1) 33.0 mm. S.L., S.C. of *Euthynnus alletteratus* (Rafinesque), BLBG.---34°35′ N., 77°03′ W., *Silver Bay* Sta. 1310, 24 Sept. 1959, (1) 113 mm. S.L., Tr. 8 fathoms, BLBG.---34°35′ N., 76°23′ W., *Silver Bay* Sta. 1250, 7 Sept. 1959, (1) 111 mm. S.L., Tr. 11–10 fathoms, BLBG.---34°34′ N., 76°36′ W., *Silver Bay* Sta. 1315, 27 Sept. 1959, (2) 83.4 mm. and 105 mm. S.L., Tr. 8 fathoms, BLBG.---34°33′ N., 77°06′ W., *Silver Bay* Sta. 1309, 24 Sept. 1959, (1) 104 mm. S.L., Tr. 9 fathoms, BLBG.---34°32′ N., 76°33′ W., *Silver Bay* Sta. 1317, 27 Sept. 1959, (2) 77.6 and 86.6 mm. S.L., Tr. 8 fathoms, BLBG.---34°32′ N., 76°49′ W., *Silver Bay* Sta. 1293, 23 Sept. 1959, (1) 181 mm. S.L., Tr. 10–11 fathoms, BLBG.---34°32′ N., 76°49′ W., *Silver Bay* Sta. 1293, 23 Sept. 1959, (9) 79.9–105 mm. S.L , Tr. 10–11 fathoms, BLBG.---34°32′ N., 75°57′ W., *Silver Bay* Sta. 1269, 12 Sept. 1959, (1) 94.5 mm. S.L., Tr. 25 fathoms, BLBG.---34°32′ N., 75°53′ W., *Silver Bay* Sta. 1268, 11 Sept. 1959, (4) 53.4–172 mm. S.L., Tr. 31–30 fathoms, BLBG.---34°31′ N., 76°51′ W., *Silver Bay* Sta. 1259, 10 Sept. 1959, (2) 84.0 and 89.2 mm. S.L., Tr. 11 fathoms, BLBG.---34°31′ N., 76°53′ W., *Silver Bay* Sta. 1239, 6 Sept. 1959, (4) 74.0–102 mm. S.L., Tr. 14–12 fathoms, BLBG.---34°29′ N., 76°49′ W., *Silver Bay* Sta. 1305, 24 Sept. 1959, (4) 97.1–163 mm. S.L., Tr. 12 fathoms, BLBG.---34°29′ N., 76°57′ W., *Silver Bay* Sta. 1307, 24 Sept. 1959, (6) 76.1–126 mm. S.L., Tr. 12 fathoms, BLBG.---34°27′ N., 76°53′ W., *Silver Bay* Sta. 1306, 24 Sept. 1959, (5) 98.5–172 mm. S.L., Tr. 12 fathoms, BLBG.---34°26′ N., 77°05′ W., *Silver Bay* Sta. 1308, 24 Sept. 1959, (11) 89.1–128 mm. S.L., Tr. 9–10 fathoms, BLBG.---34°25′ N., 76°51′ W., *Silver Bay* Sta. 1294, 23 Sept. 1959, (4) 96.3–171 mm. S.L., Tr. 12–13 fathoms, BLBG.---34°24′ N., 76°46′ W., *Silver Bay* Sta. 1238, 6 Sept. 1959, (3) 84.0–191 mm. S.L., Tr. 14–12 fathoms, BLBG.---34°23′ N., 76°54′ W., *Silver Bay* Sta. 1295, 23 Sept. 1959, (2) 179 and 189 mm. S.L., Tr. 13–15 fathoms, BLBG.---34°23′ N., 76°54′ W., *Silver Bay* Sta. 1295, 23 Sept. 1959, (3) 75.2–96.7 mm. S.L., Tr. 13–15 fathoms, BLBG.---34°22′ N., 77°09′ W., *Gill* Cr. 3, Reg. 68, 11 Aug. 1953, (48) 7.5–32.5 mm. S.L., D.N., BLBG.---34°22′ N., 75°38′ W., *Gill* Cr. 8, Reg. 74, 30 Sept. 1954, (6) 12.0–23.5 mm. S.L., D.N., BLBG.---34°22′ N., 76°13′ W., *Silver Bay* Sta. 1248, 7 Sept. 1959, (2) 86.3 and 96.4 mm. S.L., Tr. 13–15 fathoms, BLBG.---34°22′ N., 76°41′ W., *Silver Bay* Sta. 1237, 6 Sept. 1959, (9) 73.6–93.3 mm. S.L., Tr. 14–15 fathoms, BLBG.---34°21′ N., 76°34′ W., *Silver Bay* Sta. 1299, 23 Sept. 1959, (4) 49.0–61.6 mm. S.L., Tr. 14 fathoms, BLBG.---34°21′ N., 77°34′ W., *Silver Bay* Sta. 1227, 4 Sept. 1959, (5) 93.7–188 mm. S.L., Tr. 7–8 fathoms, BLBG.---34°19′ N., 77°19′ W., *Silver Bay* Sta. 1228, 5 Sept. 1959, (4) 87.1–79.4 mm. S.L., Tr. 10 fathoms, BLBG.---34°18′ N., 76°32′ W., *Gill* Cr. 3, Reg. 70, 12 Aug. 1953, (16) 17.0–49.0 mm. S.L., D.N., BLBG.---34°16′ N., 77°34′ W., *Silver Bay* Sta. 1226, 4 Sept. 1959, (5) 79.0–157 mm. S.L., Tr. 8–7 fathoms, BLBG.---34°15′ N., 77°07′ W., *Silver Bay* Sta. 1229, 5 Sept. 1959, (17) 11.0–17.8 mm. S.L., M.L.N., BLBG.---34°14′ N., 76°01′ W., *Silver Bay* Sta. 1247, 7 Sept. 1959, (3) 68.5–97.3 mm. S.L., Tr. 33–24 fathoms, BLBG.---34°13′ N., 76°48′ W., *Silver Bay* Sta. 1296, 23 Sept. 1959, (6) 109–168 mm. S.L., Tr. 17 fathoms, BLBG.---34°10′ N., 77°30′ W., *Gill* Cr. 8, Reg. 67, 28 Sept. 1954, (11) 10.0–21.5 mm. S.L., D.N., BLBG.---34°10′ N., 76°15′ W., *Silver Bay* Sta. 1245, 7 Sept. 1959, (1) 91.2 mm. S.L., Tr. 22 fathoms, BLBG.---34°09′ N., 76°35′ W., *Silver Bay* Sta. 1297, 23 Sept. 1959, (5) 94.7–211 mm. S.L., Tr. 20 fathoms, BLBG.---34°09′ N., 76°55′ W., *Silver Bay* Sta. 1230, 5 Sept. 1959, (1) 85.0 mm. S.L., Tr. 17 fathoms, BLBG.---34°07′ N., 76°32′ W., *Silver Bay* Sta. 1298, 23 Sept. 1959, (2) 94.5 and 106 mm. S.L., Tr. 19 fathoms, BLBG.---34°06′ N., 77°46′ W., *Silver Bay* Sta. 1213, 2 Sept. 1959, (5) 76.0–186 mm. S.L., Tr. 7–8 fathoms, BLBG.---34°05′ N., 76°45′ W., *Silver Bay* Sta. 1231, 5 Sept. 1959, (1) 87.6 mm. S.L., Tr. 20 fathoms, BLBG.---34°04′ N., 76°14′ W., *Gill* Cr. 7, Reg. 71, 10 July 1954, (13) 12.5–34.0 mm. S.L., D.N., BLBG.---34°03′ N., 77°50′ W., *Silver Bay* Sta. 1212, 2 Sept. 1959, (3) 88.4–180 mm. S.L., Tr. 5–6 fathoms, BLBG.---34°02′ N., 76°16′ W., *Gill* Cr. 8, Reg. 71, 29 Sept. 1954, (6) 13.0–21.0 mm. S.L., D.N., BLBG.---34°02′ N., 77°35′ W., *Silver Bay* Sta. 1214, 3 Sept. 1959, (7) 141–175 mm. S.L., Tr. 11 fathoms, BLBG.---34°01′ N., 76°37′ W., *Silver Bay* Sta. 1316, 27 Sept. 1959, (1) 119 mm. S.L., Tr. 9 fathoms, BLBG.---33°57′ N., 77°11′ W., *Gill* Cr. 8, Reg. 66, 28 Sept. 1954, (3) 11.0–14.5 mm. S.L., D.N., BLBG.---33°57′ N., 77°01′ W., *Silver Bay* Sta. 1222, 4 Sept. 1959, (4) 166–182 mm. S.L., Tr. 17–16 fathoms, BLBG.---33°57′ N., 77°01′ W., *Silver Bay* Sta. 1222, 4 Sept. 1959, (1) 11.5 mm. S.L., M.L.N., BLBG.---33°57′ N., 77°13′ W., *Gill* Cr. 3, Reg. 66, 11 Aug. 1953, (42) 8.4–52.5 mm. S.L., D.N., BLBG.---33°56′ N., 77°20′ W., *Silver Bay* Sta. 1215, 3 Sept. 1959, (18) 73.5–174 mm. S.L., Tr. 15 fathoms, BLBG.---33°55′ N., 77°52′ W., *Silver Bay* Sta. 1211, 2 Sept. 1959, (3) 75.1–146 mm. S.L., Tr. 5–6 fathoms, BLBG.---33°50′ N., 75°59′ W., *Gill* Cr. 7, Reg. 72, 10 July 1954, (1) 55.5 mm. S.L., D.N., BLBG.---33°50′ N., 76°55′ W., *Silver Bay* Sta. 1221, 4 Sept. 1959, (5) 117–128 mm. S.L., Tr. 20 fathoms, BLBG.---33°49′ N., 75°59′ W., *Gill* Cr. 2, Reg. 72, 10 May 1953, (1) 15.0 mm. S.L., D.N., BLBG.---33°47′ N., 77°50′ W., *Silver Bay* Sta. 1210, 2 Sept. 1959, (8) 81.5-207 mm. S.L., Tr. 8 fathoms, BLBG.---33°44′ N., 77°00′ W., *Gill* Cr. 3, Reg. 65, 11 Aug. 1953, (1) 11.5 mm. S.L., D.N., BLBG.---33°44′ N., 76°56′ W., *Gill* Cr. 8, Reg. 65, 28 Sept. 1954, (21) 12.0–26.0 mm. S.L., D.N., BLBG.---33°44′ N., 76°58′ W., *Silver Bay* Sta. 1217, 3 Sept. 1959, (9) 121–174 mm. S.L., Tr. 22–23 fathoms, BLBG.---33°43′ N., 76°56′ W., *Gill* Cr. 4, Reg. 65, 8 Nov. 1953, (1) 19.0 mm. S.L., D.N., BLBG.---33°41′ N., 77°40′ W., *Silver Bay* Sta.

1209, 2 Sept. 1959, (11) 79.7–182 mm. S.L., Tr. 11-12 fathoms, BLBG----33°29′ N., 76°40′ W., *Gill* Cr. 3, Reg. 64, 11 Aug. 1953, (107) 12.0–48.5 mm. S.L., D.N., BLBG----33°29′ N., 77°22′ W., *Silver Bay* Sta. 1205, 1 Sept. 1959, (7) 79.5–127 mm. S.L., Tr. 16–20 fathoms, BLBG----33°24′ N., 76°25′ W., *Gill* Cr. 3, Reg. 63, 11 Aug. 1953, (1) 11.5 mm. S.L., D.N., BLBG----33°22′ N., 77°38′ W., *Gill* Cr. 4, Reg. 59, 7 Nov. 1953, (1) 40.0 mm. S.L., D.N., BLBG----33°21′ N., 77°24′ W., *Silver Bay* Sta. 1204, 1 Sept. 1954, (4) 83.7–91.2 mm. S.L., Tr. 15-16 fathoms, BLBG----33°21′ N., 77°24′ W., *Silver Bay* Sta. 1204, 1 Sept. 1959, (21) 81.2-176 mm. S.L., Tr. 15-16 fathoms, BLBG----33°19′ N., 77°34′ W., *Gill* Cr. 3, Reg. 59 to Reg. 60, 10 Aug. 1953, (11) about 32 to 49 mm. S.L., S.C. of *Coryphaena hippurus* Linnaeus, BLBG----33°17′ N., 78°38′ W., *Gill* Cr. 8, Reg. 55, 26 Sept. 1954, (41) 9.0–48.0 mm. S.L., D.N., BLBG----33°15′ N., 76°23′ W., *Gill* Cr. 2, Reg. 63, 8 May 1953, (3) 11.0–12.5 mm. S.L., BLBG----33°03′ N., 78°21′ W., *Gill* Cr. 8, Reg. 54, 26 Sept. 1954, (121) 9.5–36.0 mm. S.L., D.N., BLBG----33°03′ N., 78°21′ W., *Gill* Cr. 7, Reg. 54, 4 July 1954, (46) 8.0–45.0 mm. S.L., D.N., BLBG----33°03′ N., 77°09′ W., *Combat* Sta. 289, 20 Apr. 1957, (1) 7.0 mm. S.L., D.N., BLBG----32°58′ N., 78°15′ W., *Gill* Cr. 8, Reg. 53 to Reg. 54, 26 Sept. 1954, (1) about 10 mm. S.L., S.C. of *Euthynnus alletteratus*, BLBG----Off South Carolina, *Combat*, 18 Apr. 1957, (1) 18.0 mm. S.L., D.N., BLBG----32°54′ N., 79°16′ W., *Gill* Cr. 4, Reg. 46, 25 Oct. 1953, (2) 42.0 and 52.5 mm. S.L., D.N., BLBG----32°54′ N., 77°04′ W., *Gill* Cr. 3, Reg. 61, 10 Aug. 1953, (17) 11.5–42.5 mm. S.L., D.N., BLBG----32°54′ N., 77°04′ W., *Gill* Cr. 2, Reg. 61, 8 May 1953, (3) 10.0–12.5 mm. S.L., D.N., BLBG----32°48′ N., 78°04′ W., *Gill* Cr. 4, Reg. 53, 27 Oct. 1953, (2) 19.0 and 22.5 mm. S.L., D.N., BLBG----32°48′ N., 78°04′ W., *Gill* Cr. 5, Reg. 53, 16 Feb. 1954, (15) 11.5–26.0 mm. S.L., D.N., BLBG----32°43′ N., 76°48′ W., *Gill* Cr. 2, Reg. 62, 8 May 1953, (2) 10.0 and 11.0 mm. S.L., D.N., BLBG----32°34′ N., 77°48′ W., *Gill* Cr. 4, Reg. 52, 26 Oct. 1953, (14) 10.0–42.5 mm. S.L., D.N., BLBG----32°34′ N., 77°48′ W., *Gill* Cr. 8, Reg. 52, 26 Sept. 1954, (16) 14.0–41.0 mm. S.L., D.N., BLBG----32°27′ N., 78°06′ W., *Combat* Sta. 297, 21 Apr. 1957, (3) 14.5–17.5 mm. S.L., D.N., BLBG----32°27′ N., 78°06′ W., *Combat* Sta. 297, 21 Apr. 1957, (3) 15.0–17.5 mm. S.L., D.N., BLBG----32°26′ N., 78°43′ W., *Gill* Cr. 7, Reg. 48, 3 July 1954, (3) 6.0–11.5 mm. S.L., D.N., BLBG----32°24′ N., 78°44′ W., *Gill* Cr. 3, Reg. 48, 6 Aug. 1953, (4) 16.5–43.5 mm. S.L., BLBG----32°24′ N., 78°45′ W., *Gill* Cr. 8, Reg. 48, 25 Sept. 1954, (17) 7.0–23.5 mm. S.L., D.N., BLBG----32°11′ N., 78°27′ W., *Gill* Cr. 5, Reg. 49, 15 Feb. 1954, (5) 16.0–33.0 mm. S.L., D.N., BLBG----32°10′ N., 78°28′ W., *Gill* Cr. 7, Reg. 49, 4 July 1954, (1) 12.0 mm. S.L., D.N., BLBG----31°56′ N., 78°10′ W., *Gill* Cr. 8, Reg. 50, 26 Sept. 1954, (16) 14.0–41.0 mm. S.L., D.N., BLBG----31°41′ N., 80°35′ W., *Gill* Cr. 4, Reg. 36, 21 Oct. 1953, (2) 29.0 and 46.5 mm. S.L., P.T., BLBG----31°41′ N., 80°35′ W., *Gill* Cr. 4, Reg. 36, 21 Oct. 1953, (37) 16–48.5 mm. S.L., D.N., BLBG----31°40′ N., 80°20′ W., *Gill* Cr. 8, Reg. 37, 21 Sept. 1954, (10) 24.0–40.0 mm S.L., D.N., BLBG----31°38′ N., 80°14′ W., *Gill* Cr. 4, Reg. 37, 22 Oct. 1953, (336) 10.0–37.5 mm. S.L., D.N., BLBG----31°38′ N., 80°14′ W., *Gill* Cr. 3, Reg. 37, 5 Aug. 1953, (2) 23.5 and 34.0 mm. S.L., D.N., BLBG----31°38′ N., 80°15′ W., *Gill* Cr. 7, Reg. 37, 2 July 1954, (28) 8.0–50.0 mm. S. L., D.N., BLBG----31°36′ N., 79°51′ W., *Gill* Cr. 8, Reg. 38, 21 Sept. 1954, (7) 17.5–29.0 mm. S.L., D.N., BLBG----31°36′ N., 79°52′ W., *Gill* Cr. 7, Reg. 38, 2 July 1954, (7) 6.5–21.5 mm. S.L., D.N., BLBG----31°34′ N., 79°28′ W., *Gill* Cr. 4, Reg. 39, 24 Oct. 1953, (1) 20.5 mm. S.L., M.L.N., BLBG----31°34′ N., 79°28′ W., *Gill* Cr. 4, Reg. 39, 24 Oct. 1953, (1) 15.0 mm. S.L., D.N., BLBG----31°33′ N., 79°27′ W., *Gill* Cr. 8, Reg. 39, 21 Sept. 1954, (29) 9.0–20.0 mm. S.L., D.N., BLBG----31°32′ N., 79°28′ W., *Gill* Cr. 3, Reg. 39, 5 Aug. 1953, (4) 13.5–24.0 mm. S.L., D.N., BLBG----31°21′ N., 80°52′ W., *Gill* Cr. 4, Reg. 35, 21 Oct. 1953, (28) 21.5–54.0 mm. S.L., M.L.N., BLBG----31°20′ N., 80°53′ W., *Gill* Cr. 8, Reg. 35, 20 Sept. 1954, (2) 21.5 and 27.5 mm. S.L., D.N., BLBG----St. Simons Island, Ga., 5 Oct. 1955, (280) 20.5–43.0 mm. S.L., Sn., BLBG----St. Simons Island, Ga., 14 Aug. 1955, (12) 9.0–23.0 mm. S.L., Sn., BLBG----St. Simons Island, Ga., 26 Dec. 1957, (1) 19.0 mm. S.L., Sn., BLBG----St. Simons Island, Ga., 11 Oct. 1957, (1) 22.5 mm. S.L., Sn., BLBG----St. Simons Island, Ga., 26 Sept. 1957, (2) 20.5 and 22.0 mm. S.L., Sn., BLBG----St. Simons Island, Ga., 27 Aug. 1957, (1) 18.5 mm. S.L., Sn., BLBG----St. Simons Island, Ga., 26 July 1957, (26) 16.5–28.0 mm. S.L., Sn., BLBG----St. Simons Island, Ga., 15 July 1957, (1) 15.9 mm. S.L., Sn., BLBG----St. Simons Island, Ga., 16 May 1957, (15) 20.0–33.0 mm. S.L., Sn., BLBG----St. Simons Island, Ga., 2 May 1957, (2) 15.0 and 25.0 mm. S.L., Sn., BLBG----St. Simons Island, Ga., 27 Apr. 1957, (3) 13.5–47.0 mm. S.L., Sn., BLBG----St. Simons Island, Ga., 16 Apr. 1957, (2) 18.5 and 22.5 mm. S.L., Sn., BLBG----St. Simons Island, Ga., 18 Mar. 1957, (1) 27.5 mm. S.L., Sn., BLBG----St. Simons Island, Ga., 20 June 1958, (2) 15.5 and 16.0 mm. S.L., Sn., BLBG----Jekyll Island Causeway, Ga., 26 Sept. 1957, (3) 17.0–21.5 mm. S.L., Sn., BLBG----Jekyll Island, Ga., 6 Aug. 1959, (1) 57.5 mm. S.L., BLBG----Jekyll Island, Ga., 18 Feb. 1959, (1) 34.5 mm. S.L., Sn., BLBG----Commercial Trawling Area, Brunswick, Ga., 20 Oct. 1955, (1) 59.0 mm. S.L., Tr., BLBG----31°00′ N., 80°23′ W., *Gill* Cr. 4, Reg. 32, 16 Oct. 1953, (441) 12.5–52.0 mm. S.L., D.N., BLBG----31°00′ N., 80°46′ W., *Gill* Cr. 4, Reg. 33, 16 Oct. 1953, (72) 9.5–46.0 mm. S.L., D.N., BLBG----31°00′ N., 80°46′ W., *Gill* Cr. 8, Reg. 33, 15 Sept. 1954, (6) 20.5–32.0 mm. S.L., D.N., BLBG----31°00′ N., 80°23′ W., *Gill* Cr. 7, Reg. 32, 27 June 1954, (36) 9.5–26.0 mm. S.L., D.N., BLBG----31°00′ N., 80°46′ W., *Gill* Cr. 7, Reg. 33, 27 June 1954, (6) 30.0–40.5 mm. S.L., D.N., BLBG----31°00′ N., 80°00′ W., *Gill* Cr. 7, Reg. 31, 27 June 1954, (10) 8.5–17.0 mm. S.L., D.N., BLBG----31°00′ N., 81°08′ W., *Gill* Cr. 4, Reg. 34, 17 Oct. 1953, (6) 19.0–29.0 mm. S.L., D.N., BLBG----30°59′ N., 79°14′ W., to 31°00′ N., 79°36′ W., *Gill* Cr. 8, Reg. 29 to Reg. 30, 15 Sept. 1954, (5) 14.0–27.5 mm. S.L., D.N., BLBG----30°58′ N., 79°38′ W., *Gill* Cr. 7, Reg. 30, 27 June 1954, (2) 13.0 and 40.0 mm. S.L., D.N., BLBG----30°20′ N., 79°26′ W., *Gill* Cr. 4, Reg. 28, 16 Oct. 1953, (2) 19.0 and 22.5 mm. S.L., D.N., BLBG----30° 20′ N., 80°35′ W., *Gill* Cr. 3, Reg. 25, 28 July 1953, (1) 11.5 mm. S.L., D.N., BLBG.---30°20′ N., 80°58′ W., *Gill* Cr. 7, Reg. 24, 26 June 1954, (8) 14.0–32.0 mm. S.L., D.N., BLBG.---30°20′ N., 80°36′ W., *Gill* Cr. 7, Reg. 25, 26 June 1954, (74) 8.5–22.5 mm. S.L., D.N., BLBG.---30°00′ N., 80°10′ W., *Silver Bay* Sta. 476, 18 June 1958, (87) 5.4–38.5 mm. S.L., D.N., BLBG.---29°48′ N., 80°12′ W., *Silver Bay* Sta. 470, 17 June 1958, (116) 6.2–21.2 mm. S.L., D.N., BLBG.---29°40′ N., 80°23′ W., *Gill* Cr. 4, Reg. 19, 14 Oct. 1953, (1) 25.0 mm. S.L., D.N., BLBG.---29°40′ N., 81°08′ W., *Gill* Cr. 8, Reg. 21, 14 Sept. 1954, (6) 15.5–34.0 mm. S.L., D.N., BLBG.---29°40′ N., 80°45′ W., *Gill* Cr. 8, Reg. 20, 14 Sept. 1954, (46) 7.5–15.5 mm. S.L., D.N., BLBG.---29°38′ N., 80°12′ W., *Combat* Sta. 474, 14 Aug. 1957, (4) 10.0–51.0 mm. S.L., D.N., BLBG.---29°38′ N., 80°09′ W., *Silver Bay* Sta. 471, 17 June 1958, (59) 5.6–33.8 mm. S.L., D.N., BLBG.---29°31′ N., 80°31′ W., *Combat* Sta. 347, 2 June 1957, (4) 124–155 mm. S.L., Tr. 18 fathoms, BLBG.---29°29′ N., 80°10′ W., *Combat* Sta. 490, 19 Aug. 1957, (2) 16.5 and 34.0 mm. S.L., D.N., BLBG.---29°29′ N., 80°09′ W., *Combat* Sta. 485, 18 Aug. 1957, (5) 15.5–38.0 mm. S.L., D.N., BLBG.---29°26′ N., 80°08′ W., *Combat* Sta. 315, 27 Apr. 1957, (2) 13.0 and 21.0 mm. S.L., D.N., BLBG.---29°22′ N., 80°05′ W., *Silver Bay* Sta. 227, 24 Nov. 1957, (3) 11.5–15.0 mm. S.L., D.N., BLBG.---29°20′ N., 80°04′ W., *Combat* Sta. 316, 27 Apr. 1957, (1) 8.5 mm. S.L., D.N., BLBG.---29°10′ N., 80°19′ W., *Combat* Sta. 336, 1 June 1957, (1) 122 mm. S.L., Tr. 25 fathoms, BLBG.---29°10′ N., 80°19′ W., to 29°19′ N., 80°15′ W., *Combat* Sta. 336–337, 1 June 1957, (62) 10.6–28.7 mm. S.L., D.N., BLBG.---29°07′ N., 80°25′ W., *Gill* Cr. 8, 28 Aug. 1954, (1) 22.0 mm. S.L., S.C. of *Euthynnus alletteratus*, BLBG.---29°00′ N., 79°48′ W., *Gill* Cr. 4, Reg. 15, 14 Oct. 1953, (1) 16.5 mm. S.L., D.N., BLBG.---29°00′ N., 80°32′ W., *Gill* Cr. 4, Reg. 13, 14 Oct. 1953, (1) 31.0 mm. S.L., D.N., BLBG.---29°00′ N., 80°10′ W., *Gill* Cr. 4, Reg. 14, 14 Oct. 1953, (32) 17.0–34.0 mm. S.L., D.N., BLBG.---29°00′ N., 79°26′ W., *Gill* Cr. 4, Reg. 16, 14 Oct. 1953, (23) 13.5–27.0 mm. S.L., D.N., BLBG.---29°00′ N., 80°32′ W., *Gill* Cr. 8, Reg. 13, 12 Sept. 1954, (6) 22.5–30.0 mm. S.L., D.N., BLBG.---Port Canaveral Anchorage, Fla., *Silver Bay*, 22–23 Nov. 1957, (1) 10.5 mm. S.L., D.N., BLBG.---Port Canaveral Anchorage, Fla., *Combat*, (1) 20.0 mm. S.L., D.N., BLBG.---27°40′ N., 80°04′ W., *Gill* Cr. 4, Reg. 5, 12 Oct. 1953, (3) 15.0–39.5 mm. S.L., M.L.N., BLBG.---27°20′N., 80°02′W., *Gill* Cr. 4, Reg. 4, 12 Oct. 1953, (3) 14.0–47.0 mm. S.L., D.N., BLBG.---27°14′ N., 79°50′ W., *Combat* Sta. 462, 29 July 1957, (10) 12.2–14.4 mm. S.L., D.N., BLBG.---26°58′ N., 79°40′ W., *Gill* Cr. 4, Reg. 2, 12 Oct. 1953, (9) 13.2–39.2 mm. S.L., D.N., BLBG.---26°47′ N., 79°53′ W., *Combat* Sta. 459, 28 July 1957, (9) 11.5–61.0 mm. S.L., D.N., BLBG.---26°37′ N., 79°51′ W., *Combat* Sta. 458, 28 July 1957, (1) 12.0 mm. S.L., D.N., BLBG.---25°16′ N., 80°07′ W., *Combat* Sta. 457, 26 July 1957, (12) 10.0–40.5 mm. S.L., D.N., BLBG.---25°13′ N., 80°10′ W., *Combat* Sta. 455, 26 July 1957, (16) 13.0–51.1 mm. S.L., D.N., BLBG.---25°11′ N., 79°56′ W., *Combat Sta.* 443, 22 July 1957, (1) 49.5 mm. S.L., D. N., BLBG.---25°11′ N., 79°56′ W., *Combat* Sta. 443, 22 July 1957, (1) 49.0 mm. S.L., D.N., BLBG.---25°10′ N., 80°02′ W., *Combat* Sta. 438, 22 July 1957, (70) 8.6–56.4 mm. S.L., D.N., BLBG.---East coast of Florida, *Combat* Sta., (5) 111–143 mm. S.L., Tr., BLBG.---Gulf Stream, (1) 100 mm. S.L., CAS 12824.--- 24°13′ N., 81°42′ W., *Combat* Sta. 436, 21 July 1957, (9) 18.0–42.0 mm. S.L., D.N., BLBG.---Key West, Fla., (1) 50.5 mm. S.L., collected by D. S. Jordan, SU 2358.---Loggerhead Key, Fla., (2) 81.0 and 97.5 mm. S.L., Tr., UF.---Sanibel Island, Fla., 19 Aug. 1959, (2) 36.0 and 42.5 mm. S.L., Sn., BLBG.---Sanibel Island, Fla., 17 Aug. 1959, (1) 40.5 mm. S.L., Sn., BLBG.---Sanibel Island, Fla., 14 Aug. 1959, (26) 20.5–50.0 mm. S.L., Sn., BLBG.---Sanibel Island, Fla., 14 Aug. 1959, (12) 18.6–49.3 mm. S.L., Sn., BLBG.---Gasparilla Bay, Fla., 17 Jan. 1958, (1) 145 mm. S.L., CHML.---Placida, Fla., 1 Jan. 1955, (1) 158 mm. S.L., CHML.---Englewood, Fla., Mar. 1958, (1) 167 mm. S.L., CHML.---Lemon Bay, Fla., 28 Sept. 1955, (1) 143 mm. S.L., CHML.---Tarpon Springs, Fla., Mar. 1930, (1) 151 mm. S.L., UF 4192.---Cedar Keys, Fla., 19 June 1949, (7) 32.8–66.6 mm. S.L., UF.---Cedar Keys, Fla., 19 June 1949, (5) 52.0–66.5 mm. S.L., UF.---Cedar Keys, Fla., 18 Oct. 1953, (2) 22.7 and 27.0 mm. S.L., UF C–10–1853–4.---Cedar Keys, Fla., 20 Sept. 1953, (2) 96.0 and 108 mm. S.L., UF 2510.---Cedar Keys, Fla., 6 Sept. 1953, (1) 102 mm. S.L., UF C–9–653–2.---Cedar Keys, Fla., 6 Sept. 1953, (1) 66.1 mm. S.L., UF C–9–653–4.---Cedar Keys, Fla., 16 Aug. 1953, (2) 61.5 and 83.0 mm. S.L., UF C–8–1653–2.---Cedar Keys, Fla., 16 Aug. 1953, (7) 63.6–88.6 mm. S.L., UF C–8–1653–4.---Cedar Keys, Fla., 16 Aug. 1953, (6) 55.5–74.1 mm. S.L., UF C–8–1653–5.---Cedar Keys, Fla., 16 Aug. 1953, (6) 56.4–74.9 mm. S.L., UF C–8–1653–5.---Cedar Keys, Fla., 16 Aug. 1953, (38) 42.3–90.2 mm. S.L., UF C–8–1653–4.---Cedar Keys, Fla., 25 July 1953, (3) 55.7–82.5 mm. S.L., UF C–7–2553–2.---Cedar Keys, Fla., 12 July 1953, (6) 61.1–89.6 mm. S.L., UF C–7–1253–4.---Cedar Keys, Fla., 12 July 1953, (1) 81.6 mm. S.L., UF C–7–1253–2.---Cedar Keys, Fla., 12 July 1953, (1) 44.8 mm. S.L., UF C–7–1253–1.---Cedar Keys, Fla., 12 July 1953, (18) 39.7–91.1 mm. S.L., UF C–7–1253–4.---Cedar Keys, Fla., 27 May 1953, (1) 53.5 mm. S.L., UF C–5–2753–3.---Cedar Keys, Fla., 27 May 1953, (1) 80.8 mm. S.L., UF C–5–2753–2.---Cedar Keys, Fla., 27 May 1953, (8) 34.3–59.9 mm. S.L., UF C–5–2753–3.---Cedar Keys, Fla., 30 June 1954, (1) 73.1 mm. S.L., UF C–6–3054–1.---Cedar Keys, Fla., 23 Nov. 1957, (7) 24.0–29.0 mm. S.L., UF.---Fort Walton, Fla., Feb.–Aug. 1959, (5) 38.0–41.0 mm. S.L., BLBG.---28°44′ N., 88°08′ W., *Oregon* Sta. 1583, 20–21 July 1956, (60) 14.9–41.3 mm. S.L., D.N., BLBG.---Aransas Anchorage, Tex., 7 June 1954, (1) 27.9 mm. S.L., UF.---5–10 miles north of San Fernando River, Mexico, 22 Mar. 1947, (1) 53.0 mm. S.L., collected by W. W. Anderson, USNM 155576.---24°50′ N., 92°35′ W., *Oregon* Sta. 2198, 23–24 June 1958, (6) 18.0–57.6 mm. S.L., D.N., BLBG.---24°05′ N., 91°46′ W., *Oregon* Sta. 2196, 22 June 1958, (6) 39.5–48.0 mm. S.L., D.N., BLBG.---22°13′ N., 89°43′ W., *Silver Bay* Sta. 404, 12 May 1958, (1) 125 mm. S.L., Tr. 25 fathoms, USNM.---24°26′ N., 81°48′15″ W., *Albatross* Sta. 2315, 15 Jan. 1885, (1) 82.5 mm. S.L., USNM 143091.---07°55′ N., 57°27′ W., *Oregon* Sta. 2247, 31 Aug. 1958, (1) 69.5 mm. S.L., BLBG.----Brazil, *Albatross,* (1) 62.0 mm. S.L., USNM 43319.----No data, (1) 83.1 mm. S.L., CAS 3437.

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34°38′ N., 74°46′ W., *Gill* Cr. 2, Reg. 80, 12 May 1953, (1) 39.6 mm. S.L., D.N., BLBG.----33°49′ N., 75°59′ W., *Gill* Cr. 2, Reg. 72, 10 May 1953, (1) 18.5 mm. S.L., D.N., BLBG.----33°29′ N., 76°40′ W., *Gill* Cr. 3, Reg. 64, 11 Aug. 1953, (1) 12.5 mm. S.L., D.N., BLBG.----33°15′ N., 76°23′ W., *Gill* Cr. 2, Reg. 63, 8 May 1953, (1) 17.2 mm. S.L., D.N., BLBG.----33°13′ N., 76°55′ W., *Combat* Sta. 290, 20 Apr. 1957, (1) 30.0 mm. S.L., D.N., BLBG.----32°40′ N., 77°40′ W., *Combat* Sta. 296, 21 Apr. 1957, (1) 43.2 mm. S.L., D.N., BLBG.----32°24′ N., 78°45′ W., *Gill* Cr. 8, Reg. 48, 25 Sept. 1954, (1) 20.0 mm. S.L., D.N., BLBG.----Bermuda, (1) 92.5 mm. S.L., collected by Beebe, USNM 178860.----31°42′ N., 79°00′ W., *Gill* Cr. 5, Reg. 41, 14 Feb. 1954, (1) 17.3 mm. S.L., D.N., BLBG.----31°29′ N., 78°41′ W., *Gill* Cr. 2, Reg. 40, 5 May 1953,(1) 24.5 mm. S.L., D.N., BLBG.---30°20′ N., 79°50′ W., *Gill* Cr. 8, Reg. 27, 14 Sept. 1954, (1) 20.5 mm. S.L., D.N., BLBG.----30°18′ N., 80°12′ W., *Gill* Cr. 3, Reg. 26, 29 July 1953, (1) 27.4 mm. S.L., D.N., BLBG.----29°48′ N., 80°12′ W., *Silver Bay* Sta. 470, 17 June 1958, (1) 34.9 mm. S.L., D.N., BLBG.----29°38′ N., 80°12′ W., *Combat* Sta. 474, 14 Aug. 1957, (18) 23.0–39.6 mm. S.L., D.N., BLBG.----29°28′ N., 80°09′ W., *Combat* Sta. 326, 30 May 1957, (1) 32.0 mm. S.L., hooked through eye on trolling rig, BLBG.----29°28′ N., 80°09′ W., *Combat* Sta. 326, 30 May 1957, (3) 34.7–38.2 mm. S.L., D.N., BLBG.----29°19′ N., 80°18′ W., *Combat* Sta. 343, 1 June 1957, (1) 41.5 mm. S.L., D.N., BLBG.----29°19′ N., 80°18′ W., *Combat* Sta. 339, 1 June 1957, (1) 37.5 mm. S.L., D.N., BLBG.----29°16′ N., 80°04′ W., *Combat* Sta. 328, 30 May 1957, (1) 49.5 mm. S.L., D.N., BLBG.----29°10′ N., 80°19′ W., *Combat* Sta. 336, 1 June 1957, (1) 39.0 mm. S.L., D.N., BLBG.----29°00′ N., 79°26′ W., *Gill* Cr. 4, Reg. 16, 14 Oct. 1953, (1) 29.0 mm. S.L., D.N., BLBG.----27°14′ N., 79°50′ W., *Combat* Sta. 462, 29 July 1957, (6) 13.6–36.8 mm. S.L., D.N., BLBG.----27°00′ N., 79°18′ W., *Gill* Cr. 3, Reg. 1, 25 July 1953, (1) 51.5 mm. S.L., D.N., BLBG.----26°58′ N., 79°40′ W., *Gill* Cr. 4, Reg. 2, 12 Oct. 1953, (5) 17.0–26.5 mm. S.L., D.N., BLBG.----26°47′ N., 79°53′ W., *Combat* Sta. 459, 28 July 1957, (14) 27.5–58.0 mm. S.L., D.N., BLBG.----25°10′ N., 80°02′ W., *Combat* Sta. 438, 22 July 1957, (2) 40.5 and 56.5 mm. S.L., D.N., BLBG.----25°16′ N., 80°07′ W., *Combat* Sta. 457, 26 July 1957, (3) 47.5–53.5 mm. S.L., D.N., BLBG.----25°13′ N., 80°10′ W., *Combat* Sta. 455, 26 July 1957, (1) 39.0 mm. S.L., Tr. 40–50 fathoms, BLBG.----25°13′ N., 80°10′ W., *Combat* Sta. 455, 26 July 1957, (1) 35.5 mm. S.L., D.N., BLBG.----28°42′ N., 86°36′ W., *Albatross,* (1) 38.5 mm. S.L., USNM 84566.----24°13′ N., 81°42′ W., *Combat* Sta. 436, 21 July 1957, (4) 36.0–54.0 mm. S.L., D.N., BLBG.----24°05′ N., 91°46′ W., *Oregon* Sta. 2196, 22 June 1958, (6) 39.0–49.5 mm. S.L., D.N., BLBG.----24°50′ N., 92°35′ W., *Oregon* Sta. 2198, 23–24 June 1958, (4) 39.0–52.5 mm. S.L., D.N., BLBG.----Cuba, (1) 108 mm. S.L., collected by Poey, USNM 9841.----Punta Colorado, Cuba, 21 May 1914, (1) 39.0 mm. S.L., Sn., USNM 82562.----St. Lucia, Windward Islands to Cayo Hutio, Cuba, 2 May 1914, (1) 82.5 mm. S.L., Tr. 2–4 fathoms, USNM 82558.----Palisadoes, Jamaica, 19 June 1957, (2) 15.0 and 16.5 mm. S.L., UF C–6–1957–1 J.----Jamaica, B.W.I., (10) 62.5–101 mm. S.L., collected by J. S. Roberts, SU 4772.----Jamaica, (2) 94.0 and 136 mm. S.L., collected by C. B. Adams, USNM 6066.---- Bizoton Wharf, Haiti, (6) 29.7–49.5 mm. S.L., collected by Beebe, USNM 178066.----Haiti, (10) 61.5–106 mm. S.L., collected by Beebe, USNM 178126.----Haiti, (1) 50.5 mm. S.L., collected by Beebe, USNM 17861.----Fox Bay, Colon, Atlantic Panama, (1) 68.5 mm. S.L., collected by Meek and Hildebrand, USNM 81510.----Fox Bay, Colon, Atlantic Panama, (1) 71.5 mm. S.L., collected by Meek and Hildebrand, USNM 81509.----16°22′ N., 83°31′ W., *Oregon* Sta. 1863, 20 Aug. 1957, (13) 11.3–21.6 mm. S.L., D.N., BLBG.----15°57′ N., 82°06′ W., *Oregon* Sta. 1935, 15 Sept. 1957, (2) 76.5 and 85.0 mm. S.L., USNM 185267.

Amanses pullus

Vineyard Sound, Mass., 3 Sept. 1914, (1) 83.0 mm. S.L., D.N., USNM 85772.----34°14′ N., 76°03′ W., *Silver Bay,* 15 Sept. 1959, (3) 41.2–57.7 mm. S.L., D.N., BLBG.----31°57′ N., 78°09′ W., *Gill* Cr. 3, Reg. 50, 6 Aug. 1953, (2) 42.0 and 46.0 mm. S.L., D.N., BLBG.----30°26′ N., 78°20′ W., *Gill* Cr. 5, 21 Jan. 1954, (1) about 42 mm. S.L., S.C. of *Coryphaena hippurus* Linnaeus, BLBG.----30°16′ N., 80°21′ W., *Combat* Sta. 70, 31 Aug. 1956, (1) 66.5 mm. S.L., Tr. 22 fathoms, TU 14749.----30°00′ N., 80°10′ W., *Silver Bay* Sta. 476, 18 June 1958, (1) 50.0 mm., M.L.N., BLBG.----29°41′ N., 80°18′ W., *Gill* Cr. 3, 28 July 1953, (1) 55.5 mm. S.L., S.C. of *Coryphaena hippurus,* BLBG.----29°38′ N., 80°12′ W., *Combat* Sta. 474, 14 Aug. 1957, (8) 45.5–92.0 mm. S.L., D.N., BLBG.----29°29′ N., 80°10′ W., *Combat* Sta. 490, 19 Aug. 1957, (2) 54.0 and 55.5 mm. S.L., D.N., BLBG.----28°18′ N., 79°28′ W., *Gill* Cr. 8, Reg. 8, 12 Sept. 1954, (1) 43.0 mm. S.L., D.N., BLBG.----28°05′ N., 78°24′ W., *Silver Bay* Sta. 446, 10 June 1958, (1) 35.0 mm. S.L., D.N., BLBG.----28°00′ N., 78°00′ W., *Gill* Cr. 3, Spc. 8, 18 July 1953, (1) 69.5 mm. S.L., D.N., BLBG.----27°41′ N., 79°40′ W., *Gill* Cr. 8, Reg. 6, 12 Sept. 1954, (1) 42.5 mm. S.L., D.N., BLBG.----27°40′ N., 79°18′ W., *Gill* Cr. 8, Reg. 7, 12 Sept. 1954, (1) 46.0 mm. S.L., D.N., BLBG.----27°02′ N., 79°23′ W., *Gill* Cr. 3, 25 July 1953, (1) about 75 mm. S.L., S.C. of *Coryphaena hippurus,* BLBG.----27°00′ N., 79°18′ W., *Gill* Cr. 6, Reg. 1, 25 Apr. 1954, (1) 66.0 mm. S.L., D.N., BLBG.----Palm Beach Inlet, Fla., 11 June 1958, (1) 158 mm. S.L., UF 7266, RC–6–1158–2.----Entrance Point, North Bimini, B.W.I., 14 July 1957, (1) 72.0 mm. S.L., TU 17801.----Settlement Point, Grand Bahama Island, *Gill* Cr. 8, 29 Aug. 1954, (3) 42.0–49.0 mm. S.L., D.N., BLBG.----Nassau, Bahamas, *Albatross,* (1) 136 mm. S.L., USNM 38375.----26°47′ N., 79°53′ W., *Combat* Sta. 459, 28 July 1957, (1) 72.0 mm. S.L., D.N., BLBG.----29°29′ N., 80°09′ W., *Combat* Sta. 485, 18 Aug. 1957, (3) 50.5–64.5 mm. S.L., D.N., BLBG.----26°11′ N., 78°15′ W., *Gill* Cr. 7, 22 June 1954, 1730, (1) 33.0 mm. S.L., S.C. of *Katsuwonus pelamis* (Linnaeus), BLBG.----26°21.2′ N., 76°46.5′ W., *Gill* Cr. 3, 23 July 1953, (1) about 51 mm. S.L., S.C. of *Coryphaena hippurus*, BLBG.___26°10′ N., 78°13′ W., *Gill* Cr. 7, 22 June 1954, 1722, (1) 44. 0 mm. S.L., S.C. of *Katsuwonus pelamis* BLBG.___26°04′ N., 78°08′ W., *Gill* Cr. 9, 15 Nov. 1954, (3) 17.5 to about 35 mm. S.L., S.C. of *Katsuwonus pelamis*, BLBG.___26°27′ N., 76°44′ W., *Gill* Cr. 7, Std., 13–14 June 1954, (1) 46.5 mm. S.L., D.N., BLBG.___25°20′ N., 77°15′ W., *Gill* Cr. 6, 19 Apr. 1954, (1) about 38 mm. S.L., S.C. of *Coryphaena hippurus*, BLBG.___25°16′ N., 80°07′ W., *Combat* Sta. 457, 26 July 1957, (1) 51.0 mm. S.L., D.N., BLBG.___24°13′ N., 81°42′ W., *Combat* Sta. 436, 21 July 1957, (2) 41.5 and 43.5 mm. S.L., D.N., BLBG.___23°40.5′ N., 76°50′ W., *Gill* Cr. 7, 19 June 1954, (2) 33.0 and 36.0 mm. S.L., S.C. of *Corphaena hippurus*, BLBG.___Tortugas, Fla., (1) 105 mm. S.L., collected by W. H. Longley, USNM 116997.___Fort Myers, Fla., 5 Sept. 1956, (1) 115 mm. S.L., spit up by a grouper, CHML.___29°26′ N., 87°32′ W., *Oregon* Sta. 792, 8 June 1953, (1) 89.0 mm. S.L., Tr. 56–57 fathoms, TU 6064.___26°10′ N., 96°25′ W., *Oregon* Sta. 1089, 4 June 1954, (1) 92.5 mm. S.L., Tr. 40 fathoms, TU 10845.___26°40′ N., 92°00′ W., *Oregon* Sta. 1035, 8 May 1954, (14) 61.0–83.0 mm. S.L., Tr. 890 fathoms, TU 10933.___24°05′ N., 91°46′ W., *Oregon* Sta. 2196, 22 June 1958, (1) 36.5 mm. S.L., D.N., BLBG.___North of Cuba, (3) 44.0–49.0 mm. S.L., collected by Beebe, USNM 178016.___Cabanas Bay, Cuba, 8–9 June 1914, (1) 46.0 mm. S.L., USNM 82566.___Cayo Hutia Light, Cuba, 12 May 1914, (1) 85.0 mm. S.L., USNM 82557.___Cuba, (1) 322 mm. S.L., USNM 32096.___Cuba, (1) 138 mm. S.L., collected by Poey, USNM 9852.___Jamaica, (2) 127 and 131 mm. S.L., collected by J. S. Roberts, SU 4943.___Ocho Rios, Jamaica, 22 June 1957, (1) 78.5 mm. S.L., UF C–6–2257–1J.___Eaton Hall Cove, Jamaica, 14 June 1958, (1) 63.0 mm. S.L., UF C–6–1458–1J.___Jamaica, (1) 325 mm. S.L., collection of Institute of Jamaica, USNM 37694.___Jamaica, (1) 288 mm. S.L., collection of Institute of Jamaica, USNM 37693.___Port-au-Prince market, Haiti, 19 Dec. 1944, (1) 100 mm. S.L., USNM 132120.___Port-au-Prince, Haiti, (5) 87.0–118 mm. S.L., collected by A. Curtis, USNM 133749.___Haiti, (1) 128 mm. S.L., collected by Beebe, USNM 178119.___Arroyo, Porto Rico, 1899, (1) 138 mm. S.L., collection of USFC, SU 8266.___Porto Rico, (1) 142 mm. S.L., collected by C. F. Cole, USNM 162780.___Porto Rico, *Fish Hawk*, (1) 136 mm. S.L., USNM 126425.___Barbuda Island, Leeward Islands, (1) 49.0 mm. S.L., collected by Beebe, USNM 183446.___Windward Island, Castries, (2) 107 and 113 mm. S.L., collected by Beebe, USNM 178598.___Port of Fortaleza, Mucuripe, Brazil, Aug. 1945, (1) 182 mm. S.L., SU 52304.___Bahia, Brazil, *Albatross*, (1) 124 mm. S.L., USNM 43323.___Port of Recife, Brazil, (2) 103 and 123 mm. S.L., SU 52305.

ADDENDUM

During the course of this study, particular attention was directed to the fact that species of the genus *Stephanolepis* were not known to occur in the Bahama Islands—despite the occurrence of both *Stephanolepis setifer* and *S. hispidus* in the currents of the Florida Current passing the west side of the Bahamas. After the manuscript was in press, 6 specimens of *Stephanolepis* were received from James E. Böhlke, Academy of Natural Sciences of Philadelphia, who had recently determined the generic identity of these specimens from the Bahaman collections of the Chaplin Bahaman Shore Fish Program:

(1) 113- and 115-mm. males and a 92.5-mm. female from Chaplin Program Station 526, Hatchet Bay, Eleuthera Island, Bahamas, 3 miles offshore, 30 ft., various stations of the *George M. Bowers*, April 20 to May 3, 1960.

(2) 106- and 113-mm. males from Chaplin Program Station 513B, Hatchet Bay, Eleuthera Island, Bahamas, 30 to 35 ft., collected by the *George M. Bowers*, February 6–13, 1960.

(3) 32.5-mm. immature specimen, ANSP 72575, New Providence, Bahamas, collected by C. C. G. Chaplin, 1949.

We would expect all these specimens to be *Stephanolepis setifer*, rather than *S. hispidus*, because our records indicate that *S. setifer* is a more offshore and insular inhabitant, while we have recorded *S. hispidus* only from continental waters; but there are inconsistancies between characters of these specimens and our recorded definition of *S. setifer* that must be pointed out.

The 32.5-mm. specimen has D. 29, A. 29, P_1 13 on both sides (more pectoral rays than previously recorded for *S. setifer*); a fairly deep body (58.1% S.L.); and a broken-line effect on the sides, but no spots on the snout or breast. On the basis of the dorsal and anal ray counts and pigment on the side, we would identify this specimen as *S. setifer*.

The 115-mm. male from Sta. 526 in Hatchet Bay has D. 30, A. 30; the 113-mm. male from this station has D. 30, A. 31 (there appears to be a minuet 31st dorsal ray); both specimens have 13 pectoral rays on each side. The pigment of these specimens is the same as that of the Cuban specimens of *S. setifer* in fig. 32, which species they undoubtedly represent. However, the high dorsal and anal fin-ray counts of the 113-mm. specimen indicate that this key character must be qualified, at least in identifying specimens from the Bahamas.

The 106-mm. male from Sta. 513B has D. 29, A. 29, P_1 12; the 113-mm. male from this station has D. 30, A. 30, P_1 13. Both specimens are faded, and lack spots on the snout and breast, but do have short dim lines on the side, and most probably are *S. setifer*.

The 92.5-mm. female (with large macroscopic eggs) from Sta. 526 has D. 30, A. 29, and P_1 12. There are no spots on the snout and breast and no broken lines on the sides; instead large dark blotches are present on the sides. The pigment and relatively large body depth (56.8% S.L.) are more like *S. hispidus* than *S. setifer*. However, considering the conflicting characters of distribution and pigmentation, and the intermediate fin-ray counts, we cannot identify this single specimen to species. (February 13, 1961.)

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EMBRYOLOGICAL STAGES IN THE SEA LAMPREY AND EFFECTS OF TEMPERATURE ON DEVELOPMENT

By George W. Piavis

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ABSTRACT

Early embryology of the sea lamprey has been subdivided into 19 stages. The stages are based largely on external morphology, behavior, and organ function. The holoblastic cleavage of sea lamprey eggs exhibited two types of third and fourth cleavages, equatorial and meridional. The open blastopore had an apparent migration over the surface of the embryo until it became the anus. Gastrulation resembles teleostean gastrulation in some characteristics and amphibian in others. Lamprey neurulation resembles teleostean neurulation more closely than it does amphibian.

Sea lamprey eggs were reared experimentally at 10 constant temperatures (at 5° intervals from 45° to 80° F., inclusive, and at 52.5° and 77.5° F.). No viable, burrowing larvae were produced at any temperature below 60° F. or above 70° F. Optimum temperature was 65° F. which yielded 78 percent survival to the burrowing stage; survival to the same stage was much lower at 60° F. (12 percent) and 70° F. (5 percent). The stage attained before all embryos were dead decreased as the temperatures were shifted in either direction from the 60°–70° F. interval. In general, developmental rate became faster, lengths of stages became shorter, and overlap between stages was lessened as temperature increased.

The evidence that sea lamprey eggs can develop successfully only within a limited temperature range suggests that unfavorable temperatures may account for the failure of certain apparently suitable streams to produce larval lampreys.

EMBRYOLOGICAL STAGES IN THE SEA LAMPREY AND EFFECTS OF TEMPERATURE ON DEVELOPMENT

By **George W. Piavis**, *Fishery Research Biologist*

The Great Lakes fisheries, the Nation's richest source of fresh-water fishes for both commercial and recreational fishing, have suffered depletion of catch and the threat of disaster. The danger has its origin in an increase in abundance of the sea lamprey, *Petromyzon marinus*, which is parisitic on and highly destructive of fish. Major goals of the Great Lakes research program of the U.S. Fish and Wildlife Service have been to develop techniques for controlling this menace, to restore the Great Lakes fishery stocks to an economically profitable level of abundance, and to sustain them at that level.

Others have outlined in detail the history of the sea lamprey within the St. Lawrence drainage and their invasion of the upper Great Lakes: (Gage, 1928; Creaser, 1932; Hubbs and Pope, 1937; Applegate and Moffett, 1955). The sequence of this invasion was summarized by Applegate (1950) as follows: 1921, Lake Erie; 1934, Lake St. Clair; 1936, Lake Huron; 1937, Lake Michigan; 1946, Lake Superior.

In planning an attack against the ever-increasing numbers of sea lampreys, practically every phase of their life history has been investigated except that of early embryology. A search of the literature reveals little on the embryology of *P. marinus*, *Lampetra fluviatilis*, *L. planeri*, and *Ichthyomyzon unicuspis*, the significant predators. Still less has been written concerning the other lampreys. Clear-cut stage designations are lacking for all lampreys. The usual embryological designations for the common early stages of development are mentioned through the gastrula stage, but even these lack clear definition.

In order to portray accurately the embryology of *P. marinus*, a study was undertaken which had as its objective the determination and definition of the various stages of development.

In these studies, staging of lamprey development has been considered essential to a better understanding of the results of the series of experiments on effects of temperature. It was immediately obvious that differences in developmental time periods would result from variations in temperatures. In order to place the entire series of temperature experiments on a common basis, an accurate series of stages was of the utmost importance.

A second objective of this study was to determine the range of temperature for development of *P. marinus* eggs as well as their optimum developmental temperature.

This work began with a preliminary investigation conducted on a part-time basis during the summer of 1954. Intensive investigations were carried on throughout the spring and summer of 1955 when temperature experiments were undertaken. Confirmatory temperature experiments at 65° F. (18.4° C.) were conducted in the summer of 1956. These latter experiments also provided materials for normal staging.

This research was conducted as part of my graduate training at Duke University while employed at Hammond Bay as a fishery research biologist by the Great Lakes Biological Laboratory of the U.S. Fish and Wildlife Service.

Embryological studies and experimental work on living materials were conducted at Hammond Bay where the facilities of the sea lamprey research laboratory were placed at my disposal by Dr. James W. Moffett, Director of the Bureau's Great Lakes Biological Laboratories, and Dr. Vernon C. Applegate, Chief of the Hammond Bay Laboratory. Sectioning and statistical work were conducted at Duke University. The University also provided me with a refrigeration unit for use at Hammond Bay and the other facilities and materials necessary to the investigation.

Dr. Edward C. Horn, Duke University, knows of my appreciation for his many criticisms and patient guidance. I wish also to thank the staff

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NOTE.—Dr. Piavis is presently Assistant Professor of Anatomy, Baltimore College of Dental Surgery, Dental School, University of Maryland, Baltimore 1, Md.

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of the Hammond Bay Laboratory, and especially John Howell, for courtesies shown me and the time spent in my behalf.

STAGES IN NORMAL DEVELOPMENT

MATERIALS AND METHODS

Eggs of the sea lamprey were taken from mature, nest-building or spawning lampreys found in either the Trout River or the Ocqueoc River, both tributary to Lake Huron, Presque Isle County, Michigan.

Spawning lampreys were seized in a forked grip which placed the lamprey between the forefinger and the middle finger while the thumb anchored the animal. Capture by hand, in this way, minimized the loss of specimens by injury. The lampreys were kept in stream water throughout the transfer from the stream to the central collecting point, and to the laboratory where they were tempered and stripped in preparation for fertilization. To condition the eggs and sperm adequately to the test temperatures the lampreys were tempered in running lake water 2 to 3 hours prior to the initiation of the experiments.

Eggs were removed rapidly from female lampreys, held by two people. One held the anterior end by placing a thumb within the oral disc, thus taking advantage of the cusps to prevent slippage. The other held the tail by means of a pair of pliers. While the lamprey was thus outstretched, a transverse slit was made with scissors in the midventral body wall at a point behind the heart and the liver, i.e., at the anterior level of the ovaries. If the females were ripe, eggs began to extrude from this initial opening, whereupon the lamprey was slit to the vent by a rapid stroke with half-open scissors. Since the eggs are completely free in the coelom of a ripe female, they were allowed merely to flow into a 10-liter battery jar which contained a few liters of lake water from the trough where the animals were tempered. Any eggs entrapped within the coelom or folds of the ovary were removed rapidly by dipping the lamprey into the water with the slit open. This method of removing the eggs was quicker and far superior to the milking procedure used by McClure (1893) and others (including the author) because the time required to clear the female of eggs was limited only by the dexterity of the operators. Furthermore, the eggs are not distorted or damaged. Blood was not introduced into the fertilization jar since the slit produced no blood providing neither the liver nor the heart was pierced.

The males were grasped in the manner described for the females. The individual who was holding the lamprey by the oral disc forced the milt from within the coelom through the genital papilla in a stream directed over the eggs in the battery jar. Two males were used for each female; four males and two females constituted the usual batch.

Immediately after the addition of sperm, the jar was provided with an air bubbler and placed in a trough previously brought to the desired temperature. The entire operation from stripping to placing in the jar was completed within 60 seconds. Twenty to 30 minutes after fertilization the eggs were washed. Washing was repeated at least two more times during the first hour to insure complete removal of excess sperm. After the first hour the eggs were apportioned among enamel pans (8″ x 12″ x 2″) or, on occasion, 4-inch glass bowls. These containers were covered with glass plates to minimize the accumulation of water-borne debris, and submerged. Circulation of water beneath the glass covers and over the developing embryos was insured by allowing a small area of the pans and bowls to remain uncovered. Care was taken not to crowd the eggs in the containers. Preliminary work had shown that eggs arranged in more than a single layer were highly susceptible to attack by fungus.

Development of the embryos took place in the pans or bowls which were held at the desired temperature in either constant-temperature troughs or in 20-gallon aquariums. Each insulated trough measured 12 feet by 2 feet by 9 inches and contained an inner-water chamber surrounded by a 3-inch outer-water chamber. Spaces beneath the metal divider provided free access between the inner and outer chambers. Water within the inner chamber was provided with air from controllable bubblers.

The troughs were equipped with thermostatically controlled heating units and refrigeration units which provided temperature control within ±0.5° F. The refrigeration tubing, the heating elements, and the thermostat bulbs lay within the 3-inch outer chamber.

Water was circulated over the thermal units by a continuously revolving 6-vane water wheel driven by a Ratiomotor. Since water flowed freely between the outer and inner chambers, the action of the thermal units was transmitted with little time lag to the inner chamber which held the container of eggs.

Heat for the high temperatures was provided by Bronwil circulators and heaters used in aquaria filled with lake water and provided with a controllable air bubbler. Bowls and pans were used to contain the eggs within the aquaria as in the troughs. Air bubblers and water circulation by the Bronwil circulators provided air for the aquaria. The circulators equipped with a contact-thermostat and thermometer can be utilized for any temperature setting from room temperature to boiling. In order to attain the maximum range from this piece of apparatus the aquaria were located within a cool room where it was expected that the ambient temperature would not rise above the desired temperature. The temperature variation for the circulator was advertised as ±0.18° F. In actual practice, however, temperature variation could not be noticed. The apparatus just described was utilized for experiments at temperatures of 65° to 80° F.; the troughs were used for temperatures from 45° to 70° F.

Prior to each experiment, troughs and aquaria were washed, air-dried, and refilled with lake water; the thermostat was then set at the desired temperature. Observations of the temperature at 5-minute intervals for a period of 4 to 8 hours and occasional readings in the remainder of a 24-hour interval, assured stabilization at the correct temperature. After the desired temperature was established, Taylor thermographs and hourly readings of total-immersion thermometers (placed on submerged rubber stoppers grooved to receive them) gave a further check. The thermometers were set in such a manner as to be readily visible without handling. Thermographs were not used with the circulator but the temperature was watched for 4 to 12 hours prior to the initiation of the experiment. Because of the small variation in temperature delivered by the circulator, a thermograph record was considered unnecessary except when the ambient temperature was expected to rise above that desired. Furthermore, a submerged thermometer was compared periodically with the contact-thermostat and thermometer.

All sampling was random throughout the experiments, and in general, the procedure varied only slightly from that outlined below. Fertilization was considered zero time; the first sample was taken 20 to 30 minutes after fertilization. Thereafter, samples were taken at the following hours: 1, 2, 3, 4, ___ 12, 14, 16, 18, 20, 24, 28, 32, 40, 48, ___ 72. After the 72d hour samples were taken at 12-hour intervals until the end of the experiment. In some of the longer experiments, samples were taken each 24 hours after about the 18th day. In addition to the samples taken during the run, all remaining eggs and larvae were kept as a final sample.

Samples of specimens were placed in Syracuse dishes and the gross morphological characteristics of the embryos were observed under a binocular dissecting microscope. The microscope was equipped with a calibrated ocular micrometer with which all measurements were made. Immediately after these observations all samples were placed in Smith's fixative[1] for 12 to 24 hours, washed in several changes of water during a 24-hour period, and preserved in a 4-percent solution of formalin. This method of fixation and preservation was most satisfactory as judged by the pliability of the heavily yolk-laden eggs after 3 years' preservation.

Specimens to be sectioned for microscopic examination were washed overnight in running tap water, stained in alum-cochineal 16 to 24 hours, then dehydrated and embedded in paraffin. Sections cut at 5 to 10 micra were mounted and counterstained in a 0.5-percent solution of fast green in 95-percent ethyl alcohol and covered permanently.

DESCRIPTION OF STAGES

The following description of stages was based on materials which were taken from all of the batches of the different temperature series; but greatest emphasis was placed on observations of the 65° F. batches. Most characteristics of embryos of the other batches were identical with those reared at 65° F. Those differences which were observed are pointed out in the discussion of the particular stage. The time intervals listed for each stage include the time between the first and last appearance of the stage in the samples reared at 65° F.

The end-points selected for each stage were established after numerous observations of both living and preserved materials. It was considered essential to be able to recognize all preserved stages at a later time as well as living stages at the moment of collection.

---

[1] Solution *A*: Potassium bichromate 0.5 gm., water 87.5 cc. Solution *B* Formalin 10 cc., glacial acetic acid 2.5 cc. Mix solutions *A* and *B* immediately before using.

In addition to the gross morphological end-points, histological examination was used on occasion to define the stage more critically. The criteria selected were such as to include also the physiological differences. Furthermore, since the status of an animal is evidenced in part through its activity and movements, natural movements or activity were incorporated as far as possible into the staging criteria.

The method of fixation and preservation proved to be suitable for recognition of practically all end-points. The normally transparent prolarvae[2] became opaque in Smith's fixative. When selected specimens were fixed and preserved in 4-percent formalin, however, retention of all pigmentation and transparency aided staging. The formalin, of course, hardened the yolk mass and the notochord enough to prevent the use of these specimens for histological preparations.

Stage 0: Ovulated but unfertilized egg

Animal-pole depression: Present but just visible.

Cellular areas: Nuclear; animal-hemisphere cytoplasm; vegetal-hemisphere cytoplasm.

Size: 1.0 ± 0.2 millimeters.

Ovulated eggs within the coelom are assigned this stage. These creamy-white eggs are surrounded by a relatively thin jelly coat which expands when the eggs are shed into water. The stickiness of this coat causes sand grains stirred up by spawners to adhere to the surface of the egg.

The surface of the unfertilized egg has a small depression in the egg membrane over the nucleus and extends into the nucleus proper. A demarcation separates the nucleus and the surrounding cytoplasm. One-third the distance down the animal-vegetal axis the cytoplasm contains another demarcation between the cytoplasm surrounding the nucleus and the remaining cytoplasm.

The egg of the sea lamprey is telolecithal in that the egg consists of a relatively large amount of yolk and the nucleus is located at the center of the animal hemisphere.

This stage is initiated when the eggs are ovulated into the coelom and ends with fertilization.

Stage 1: Zygote (fig. 1) hours 0-2

Animal-pole depression: Increases in diameter and depth; disappears within about 1 hour.

Cellular areas: Identical to stage 0.

Size: 1.0 ± 0.2 millimeters.

Fertilization membrane: Appears within 20–30 minutes after fertilization; is retained through stage 13.

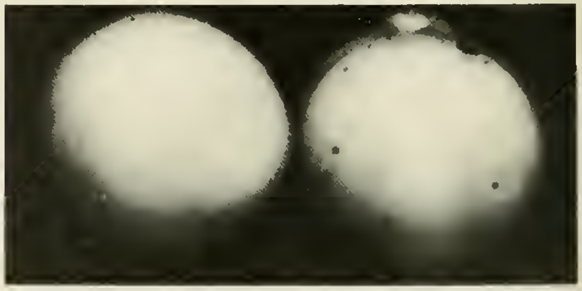

FIGURE 1.—Lateral view of stage 1, zygote, showing cellular areas.

This stage extends from the time of fertilization to the time when the fertilized egg begins to undergo first cleavage. A meridional section of a fertilized egg (fig. 2) shows the yolk platelets

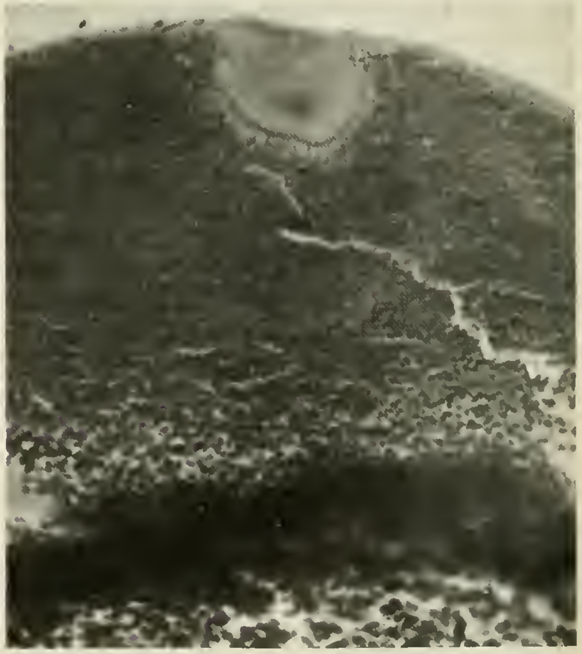

FIGURE 2.—Meridional section of stage 1 prior to formation of fertilization membrane.

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[2] Hubbs (1943) defined a prolarva as a "larva still bearing yolk." In the present work prolarva includes stages 14-17.

within the cytoplasm surrounding the nucleus and the remaining cytoplasm. The yolk of the animal and the vegetal areas differs in that the yolk platelets within the vitelline area are much larger than those in the area around the nucleus.

The depression at the animal pole seen in stage 0 persists through this stage. The first indication of significant morphological change is a noticeable deepening of this depression which will remain until about the first hour after fertilization.

Three distinct external areas indicate the presence of the three internal areas: nucleus; animal-pole cytoplasm; and vegetal-hemisphere cytoplasm. Below the nucleus the cytoplasmic area is demarcated by a band extending approximately one-third the distance down the animal-vegetal axis. The remainder of the egg consists of cytoplasm heavily laden with yolk. Each of the areas of the egg is visible both externally and internally as early as the unfertilized egg and up to the initiation of first cleavage.

Shortly after the animal-pole depression deepens, the fertilization membrane appears.

Stage 2: Two cells (fig. 3) hours 2-8

Cellular areas: Visible in the daughter cells.

Size: 1.0±0.2 millimeters.

Cleavage: First furrow appears. Prominent peaks in daughter cells. Holoblastic. Completed within 5–6 hours.

The external topography of the 2-cell stage is comparable to that of the zygote in that the nuclear, and the animal- and vegetal-hemisphere cytoplasmic areas are readily visible in both daughter cells immediately after reconstitution of the nucleus (fig. 3).

This stage begins when the animal pole of the zygote begins to furrow and dimple in preparation for first cleavage, and ends at the beginning of the second cleavage furrow and dimple at the animal pole. Cleavage is total, usually slightly unequal (fig. 4) but occasionally (less than 1 percent) grossly unequal. As mentioned above, cleavage begins as a small furrow; a slight uprising of the cell membrane lateral to the furrow produces the dimpled effect. As cytokinesis progresses the cell membrane expands to a greater and greater extent while the fertilization membrane remains unchanged. The cell membrane continues to expand until the cell reaches the stage seen in figure 3, where the expanded cell membrane can be seen as twin peaks lateral to and above the furrow. As the cleavage furrow progresses meridionally over

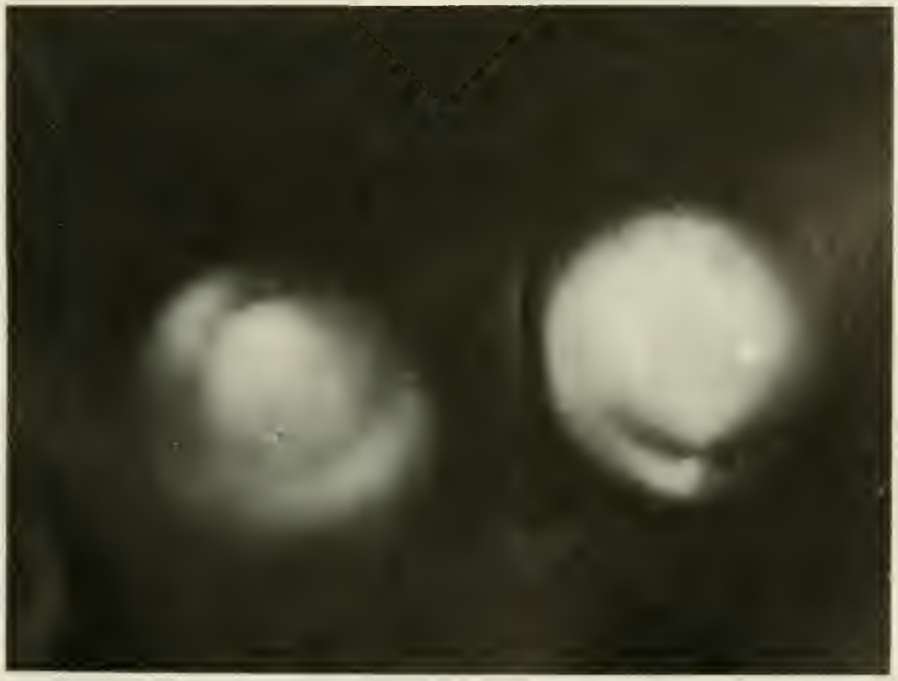

FIGURE 3.—External views of stage 2, two cells, showing the expanded cell membrane (right side) and daughter cells showing the cellular areas.

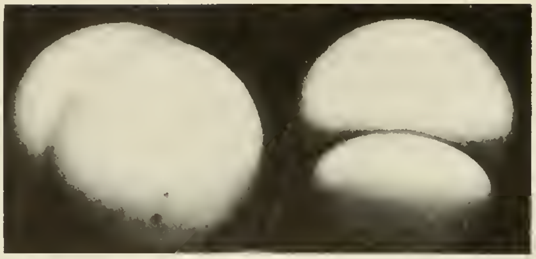

Figure 4.—External views of cleavage extremes of stage 2.

the cell, the cell membrane expands in advance of the progressing furrow.

Stage 3: Four cells (fig. 5) hours 8-11

Cellular areas: Visible in four daughter cells.

Size: 1.0±0.2 millimeters.

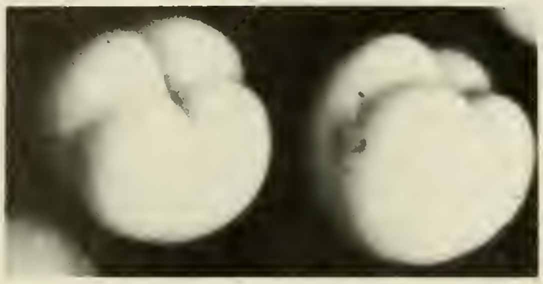

Figure 5.—Various external views of stage 3, four cells.

Cleavage: Second furrow appears: peaks are less prominent than in first division. Holoblastic. Completed within 3 hours.

Despite cellular division the three distinct topographical areas are still discernible in each of the four cells.

Stage 3 begins with the advent of the second cleavage furrow and dimple which starts in much the same manner as the first; the furrow and dimple are observed at the animal pole to either side of the first cleavage furrow and progress meridionally at right angles to the first cleavage furrow. As in stage 2, the expanding cell membranes are observed during cytokinesis.

The end-point of stage 3 is the appearance of third cleavage furrow and dimple.

Stage 4: Eight cells (fig. 6) hours 10-15

Cellular areas: Visible in meridional type cleavage.

Size: About 1.0 millimeter for equatorial division. Meridional division increases equatorial diameter and shortens meridional diameter.

Cleavage: Two types; meridional or equatorial. Holoblastic. Completed within 2 hours.

Stage 4 begins with the appearance of the third cleavage furrow, which may be either a double

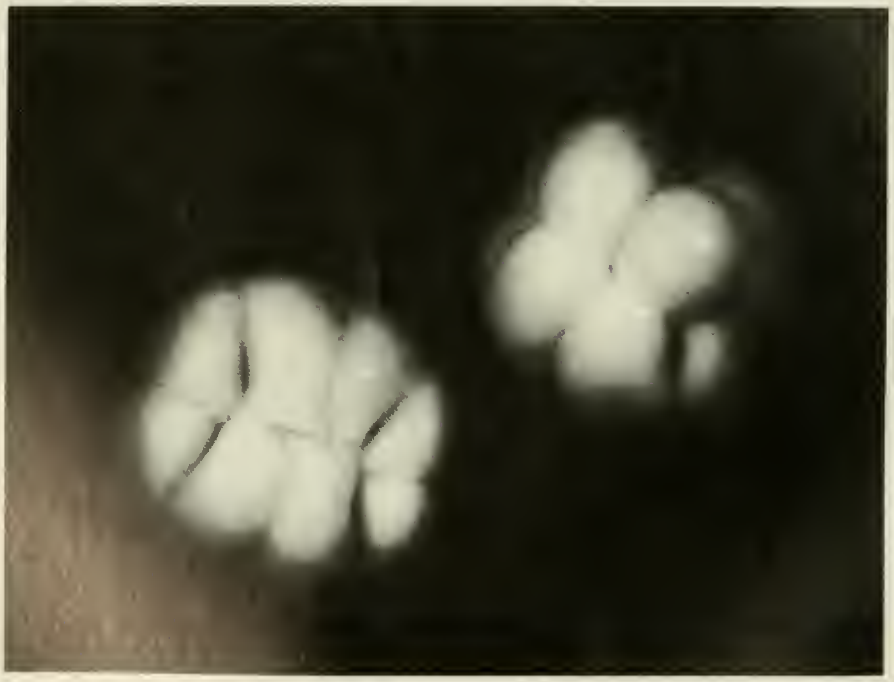

Figure 6.—Polar views of meridional and equatorial cleavages forming stage 4, eight cells.

meridional furrow or a single equatorial division. The meridional type was described by McClure (1893) for *P. marinus* eggs held at 6°–8° C. (42.8°–46.4° F.) or at room temperature, whereas both types of cleavage were found in this study. The equatorial cleavage was not mentioned by McClure, although it predominated in the present study in all experimental batches, regardless of temperature.

Embryos formed after meridional cleavage can be distinguished by the flatness at the animal pole. The nuclei are aligned four on each side of the first cleavage plane (fig. 6). In some embryos the segmentation cavity can be seen because the embryo splits along the first cleavage plane.

The flatness of stage 4 embryos formed by meridional divisions produces a large perivitelline space which facilitates removal of the fertilization membrane. The same operating space is not encountered again until stage 9.

The embryos formed by equatorial divisions have 4 micromeres resting upon 4 macromeres. In them, the space available for removal of the fertilization membrane is relatively small.

The end-point of this stage is the appearance of the fourth cleavage furrow.

Stage 5: Sixteen cells (fig. 7) hours 13-15

Cellular areas: No longer recognizable from external view.

Size: 1.0 millimeter.

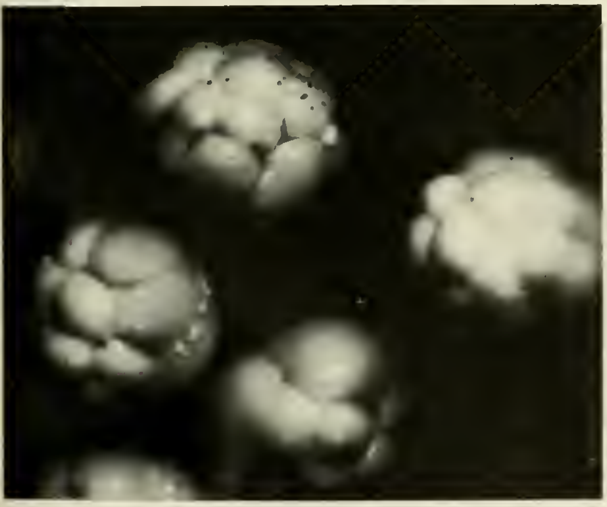

FIGURE 7.—Several views of stage 5, sixteen cells, illustrating differences in size of animal and vegetal cells.

Cleavage: Equatorial or meridional, depending upon type in stage 4. Pattern irregular. Completed within less than 2 hours.

Stage 5 begins with the appearance of the fourth cleavage, the plane of which varies according to the type of cleavage which formed stage 4; a third-stage equatorial division, near the animal pole, is followed by a fourth meridional division and vice versa. Cleavage irregularity becomes apparent during this stage; embryos composed of 9 to 16 cells are found and included in this stage.

The end-point of stage 5 is reached when the embryo is composed of 17 or more cells.

Stage 6: Thirty-two cells (fig. 8) hours 16-19

Size: 1.0 millimeter.

Cleavage: Random and indeterminate. Completed within 1 hour.

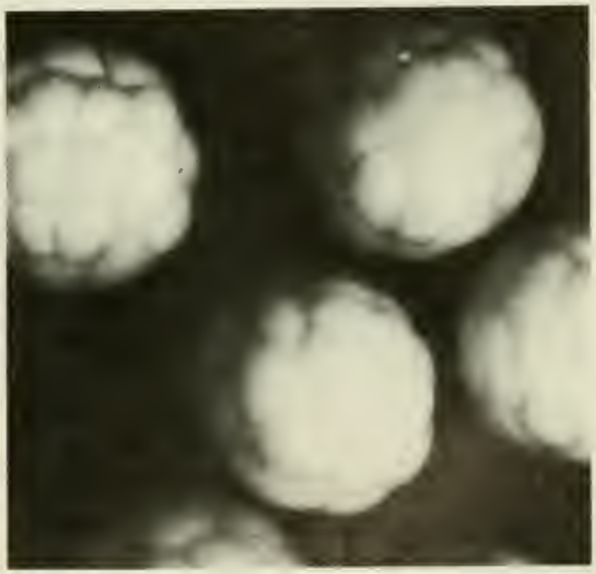

FIGURE 8.—Several polar views of stage 6, thirty-two cells.

Embryos were assigned to this stage when 17 to 32 cells were distinguishable. Cytokinesis at this point, however, became indeterminable so that the fifth cleavage appeared to take place at random. Cell counts were made on all embryos that could not be identified on the basis of relative cell sizes by comparison with both stages 5 and 7. When animal cells are compared with animal cells, and vegetal cells with vegetal cells, the cells of stage 6 embryos will be about one-half the size of stage 5 cells and approximately twice the size of stage 7 cells. The relative sizes of the animal-

and vegetal-cells can be ascertained in figure 9, a meridional section of stage 6.

The extent of the blastocoel can also be seen in figure 9. The roof of the blastocoel is composed of a single layer of relatively large animal cells whereas large vegetal cells extending from the vegetative pole to the blastocoel constitute the floor. The end-point of stage 6 is reached when the embryo has 32 cells.

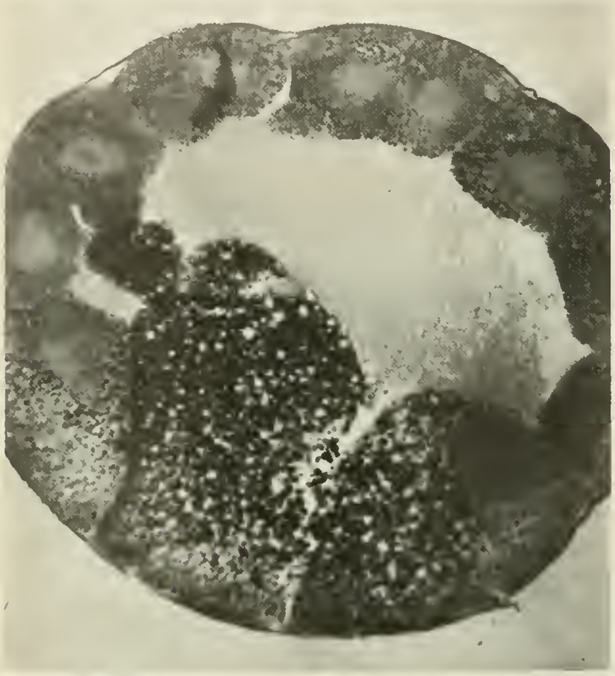

Figure 9.—Meridional section of stage 6.

Stage 7: Sixty-four cells (fig. 10) hours 19-24

Size: 1.0 millimeter.

Cleavage: Indeterminate.

Stage 7 is considered to have begun when the embryo has more than 32 cells. The cleavage continues indeterminable in this and later stages. Recognition of the stage becomes a matter of cell counts and comparison of cell sizes with those of the preceding and succeeding stages. A cursory count of the animal cells is made to get an approximate estimate of the stage to which the embryo should be assigned; the final assignment is based on a combination of cell size and cell count. As cell size diminishes the contour of the embryo becomes smoother. This change can be seen in a comparison of figures 8 and 10. The animal cells are still smaller than the vegetal cells, which have since divided and are now only about twice the size of the animal cells.

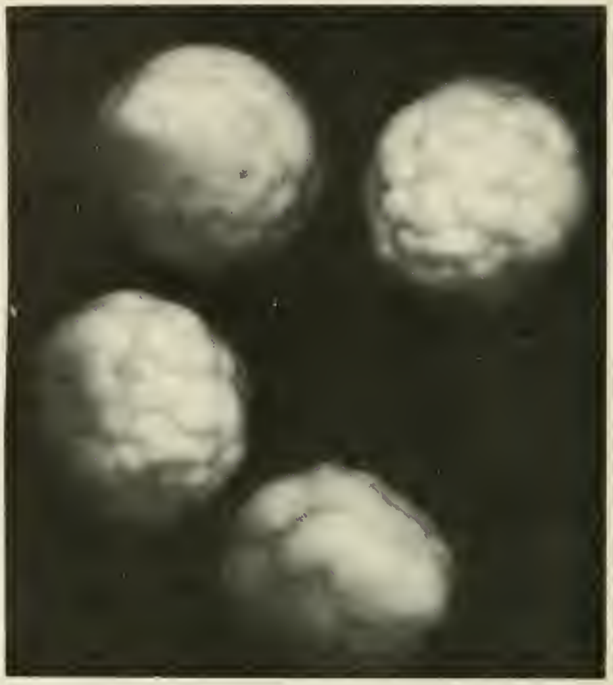

Figure 10.—Polar and lateral views of beginning stage 7, sixty-four cells.

The end-point of stage 7 is reached when the embryo has more than 64 cells. Division of all animal cells along with division of the vegetal cells can be taken as an approximate end-point.

Stage 8: Full blastula (fig. 11) hours 24-64

Size: 1.0 millimeter, increasing to 1.2–1.4 millimeters.

Cleavage: Furrows seen on individual cells.

Animal hemisphere: Becomes translucent.

Blastocoel: Visible through animal cells.

When the animal pole cells of stage 7 undergo further cell division as evidenced by further reduction in cell size and the appearance of cleavage furrows, the embryo is considered to have entered stage 8. The most striking external feature of this early phase of the stage is its contours (compare to stage 7) which become progressively smoother as the number of cell divisions increases and cell size decreases.

In the final phase of this stage the volume of the embryo increases by some 3 to 5 times. Measurements of living specimens made within a calibrated ocular micrometer at the initiation of and

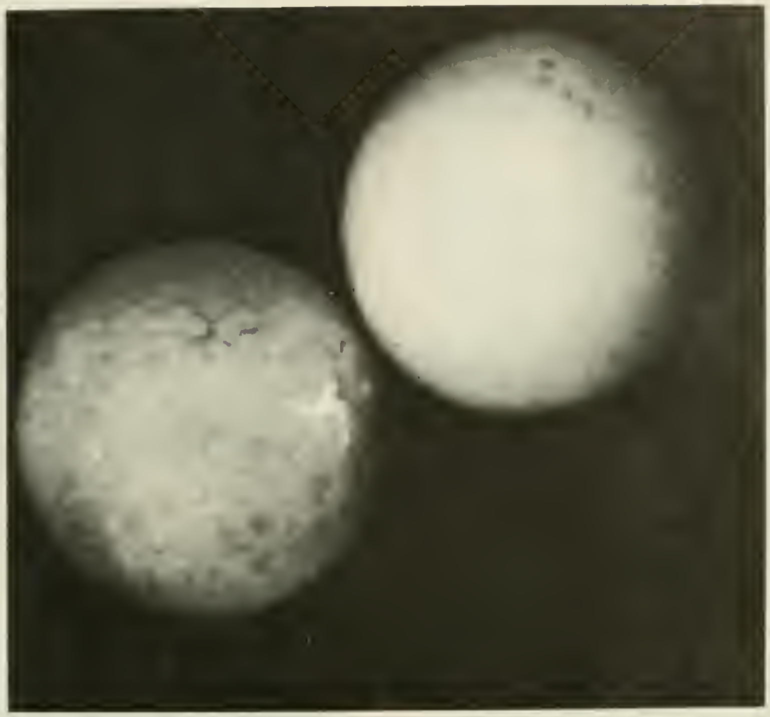

FIGURE 11.—Polar views of stage 8, full blastula, arranged to illustrate changes in cell size.

just prior to this stage were consistently about 1.0 millimeter across as viewed and measured in optical section perpendicular to the animal-vegetal axis as well as along that axis. Subsequent measurements prior to the appearance of the dorsal lip of the blastopore, the end-point of stage 8, ranged from 1.2 to 1.4 millimeters. The increase in volume is accompanied by translucency of the animal-pole cells so that the outline of the blastocoel becomes visible through approximately one-third the surface of the embryo. The size of the animal cells does not change during the expansion process; the increase of the blastocoel indicates that the expansion is due to blastocoel enlargement. The blastocoel is at its greatest volume at the end of stage 8. The animal cells are still about one-half the size of the vegetal cells. This size relation is maintained as long as the epibolizing animal cells can be compared externally with the underlying vegetal cells.

The end-point of stage 8 is the appearance of the blastopore.

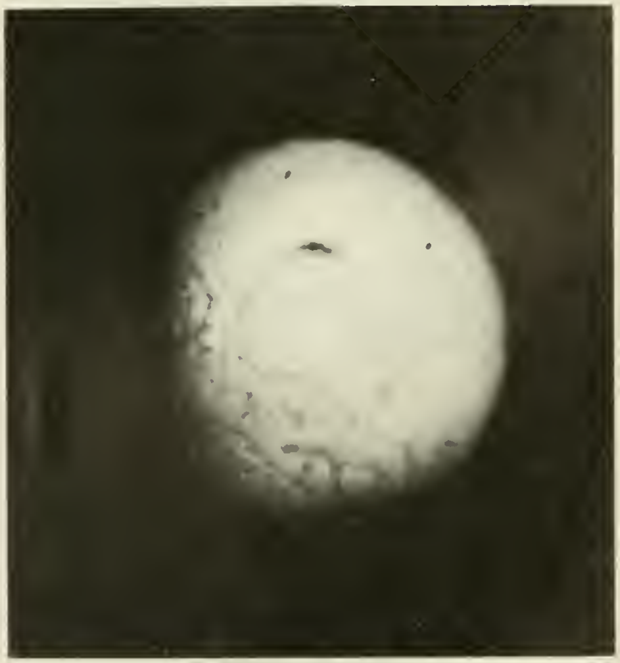

FIGURE 12.—Posterior view of stage 9, gastrula, illustrating the blastopore.

Stage 9: Gastrula (fig. 12) hours 64-104

Size: 1.2 to 1.4 millimeters decreasing to 1.0 millimeter.

Animal hemisphere: Translucent to transparent to opaque. Opacity extends progressively forward from blastopore. Begins to flatten, forming neural plate.

Blastocoel: Progressively obscured by opacity of animal hemisphere. Decreases in volume.

Blastopore: Forms as wide arched slit. Hooded as neural plate begins to form. Apparently migrates.

The translucency of the animal hemisphere of stage 8 changes to transparency after the appearance of the blastopore. Through the transparent animal hemisphere the underlying chorda-mesoderm is visible as it undergoes its morphogenetic movements. During this period the volume of the blastocoel decreases when the chorda-mesoderm reaches a position two-thirds the distance across the animal hemisphere. The most advanced portion of the chorda-mesoderm is in the mid-sagittal plane; the material in the parasagittal planes lags behind these more advanced cells. As this material progresses beneath the animal hemisphere, the dorsal lip of the blastopore progressively increases in thickness and begins an apparent migration from its original position at or near the overlap of animal and vegetal cells one-third the distance from the center of the animal hemisphere, toward the center of the animal hemisphere. As the chorda-mesoderm moves to its anteromost position in the embryo, the transparency of the animal hemisphere decreases, and the decrease in the volume of the embryo continues.

The typically circular blastopore of later stages is formed by progression of the animal cells in their epibolic movements to produce a changing pattern to the dorsal lip and, necessarily, the blastopore. At the time of the blastopore's inception the advancing margins of epibolizing cells beneath the blastopore approach each other laterally as a wide-open *V* with the apex at the center of the dorsal lip of the blastopore. As gastrulation progresses, these V-arranged margins close toward each other until only the vegetal cells below the blastopore remain uncovered. These vegetal cells are covered by epibolizing cells which move upward along the mid-sagittal plane (fig. 12).

As the chorda-mesoderm advances farther into the anterior portion of the embryo, the blastopore begins an apparent migration along the mid-sagittal plane from its original position to one located at the posterior limit of the mid-sagittal plane in stage 10. Histological comparisons between stages 8 and 9 indicate that this apparent movement resulted from reduction in the size of the blastocoel. At this time the dorsal region of the entire embryo begins to flatten and to thicken from the dorsal lip of the blastopore to the anterior region.

Stage 9 is marked by the appearance of the dorsal lip of the blastopore, a flat crescentic-shaped furrow within the overlapping line of the animal cells epibolizing over the vegetal cells. Recognition of the stage depends upon locating the blastopore half-way beneath the embryo; the observer must rotate the embryo to find it.

The end-point of stage 9 is reached when the flattening process reaches the anterior end of the embryo.

Stage 10: Neural plate and groove (fig. 13) days 4-5

Size: 1.1 to 1.3 millimeters.

Blastopore: Triangular to ovoid. Reaches its dorsalmost point.

Neural tissue: Neural plate forms and thickens. Groove and folds form.

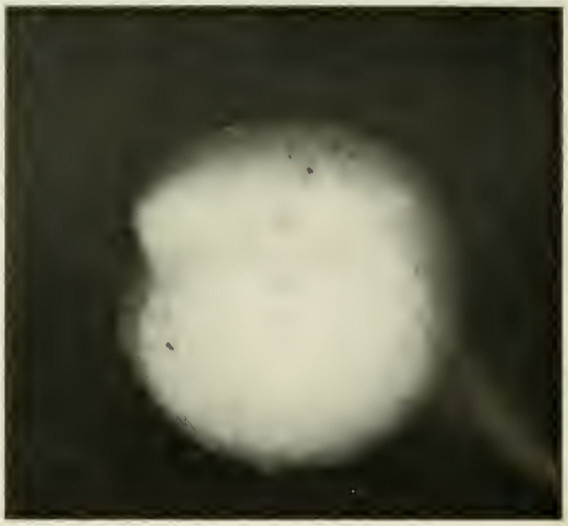

Figure 13.—Lateral view of stage 10, neural plate.

Stage 10 begins when the flattening of the dorsal ectoderm mentioned in stage 9 has reached the anterior extremity of the embryo (fig. 14). At the same time, the nearly completed blastopore is near or at the dorsalmost point of the posterior area of the mid-sagittal plane of the embryo (fig. 15). Further thickening of the depth of the flattened area follows almost immediately after the flattening of the dorsal ectoderm extends from the blastopore to the anterior region. These animal cells are no longer transparent. The ovoid to triangular

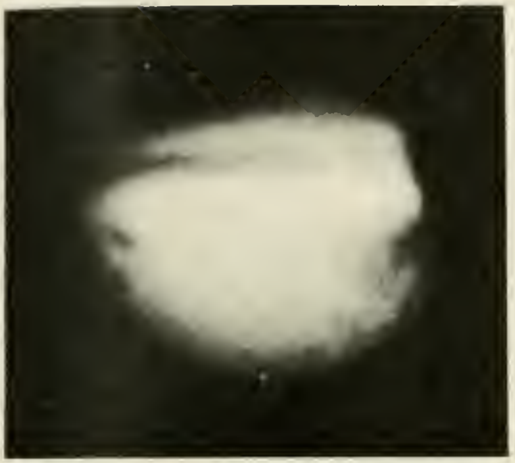

FIGURE 14.—Dorsal view of stage 10 illustrating neural groove.

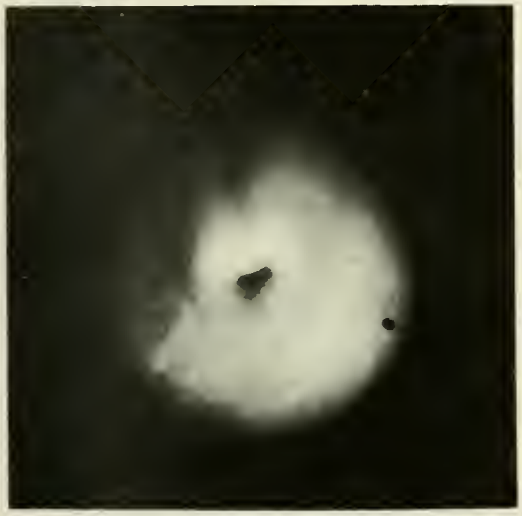

FIGURE 15.—Posterior view of stage 10 illustrating blastopore and neural plate with neural groove.

blastopore is now at the uppermost point of its apparent migration along the mid-sagittal plane and the flattened ectodermal cells (neural plate) are at the height of their thickening. Practically all the vegetal cells are covered by the epibolizing animal cells. Immediately after the neural plate thickens, the central portion of the plate begins to form a trough, producing a neural groove and fold stage (fig. 16). As the groove in the neural plate deepens the "folds" begin to approximate each other and unite. The first actual union occurs in the mid-dorsal region of the embryo. This union is the end-point for stage 10.

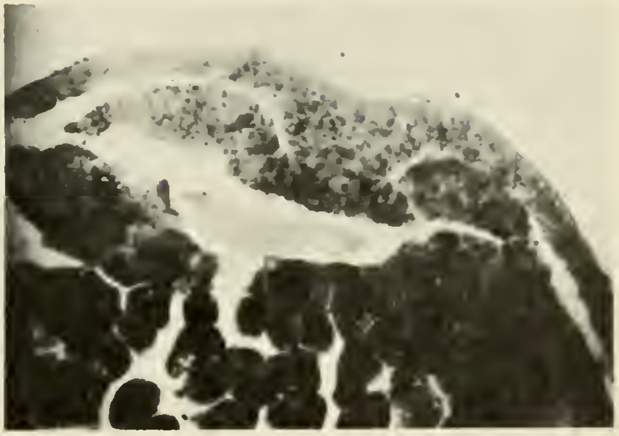

FIGURE 16.—Cross-section of stage 10

Stage 11: Neural rod (fig. 17) days 5-6

Size: 1.1 to 1.3 millimeters.

Blastopore: Circular. Apparent migration toward ventral surface of embryo.

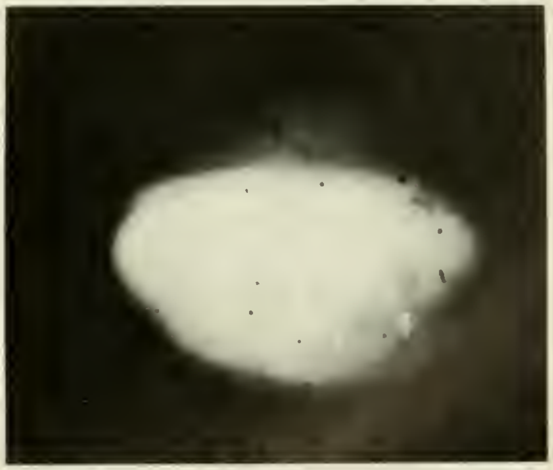

FIGURE 17.—Oblique lateral view of stage 11, neural tube.

Neural tissue: Union of folds middorsally on embryo. Neural tube lacks neurocoel, and thus is a neural rod. Becomes prominent across dorsum of embryo; circumscribes approximately two-thirds of embryo.

In the late phase of this stage the dorsoposteriorly located, circular blastopore begins an apparent migration toward the ventral surface accompanied by a similar ventral movement of the prospective head. Toward the end of this stage the circular blastopore is at the ventralmost point of the posterior as contrasted with its earlier position at the dorsalmost point of the posterior. These movements continue until the neural rod occupies approximately two-thirds of the circumference of the embryo.

The union of the folds marks the beginning of stage 11. The neural plate begins to round up and appears in external view to have become a neural tube with anterior and posterior neuropores. This appearance is a result of the apparently simultaneous, progressive union of the folds in anterior and posterior directions from the site of first union, the middorsum.

The external morphology of this stage is as deceptive as that of the preceding stage since histological examinations reveal that the neural tube does not possess a neurocoel; in reality the neural tube is a neural rod as described by Shipley (1885). In the anteromost region the neural rod seems to elevate from the surrounding and underlying tissue.

The end-point of this stage is reached when the anterior region is raised above the globular yolk mass.

Stage 12: Head (fig. 18) days 6-8

Size: 1.1 to 1.4 millimeters.

Blastopore: Below posteriormost point of neural rod, at ventral surface of embryo. Circular.

Neural tissue: Very prominent from head to blastopore. Neurocoel over presumptive pharynx.

Head: Elevated from yolk mass. Free length approximately 1.0 millimeter.

Yolk: Globular as in preceding stages.

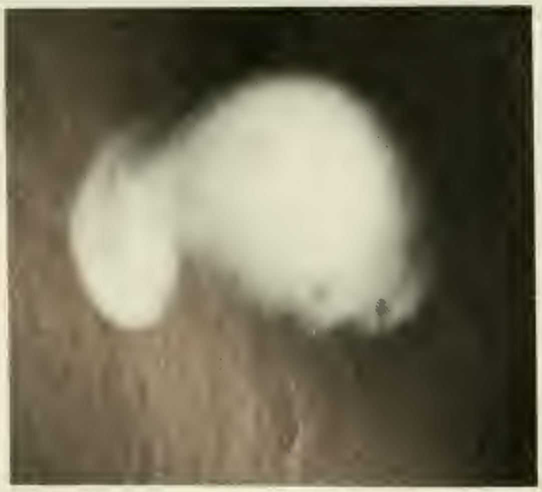

Figure 18.—Lateral view of stage 12, head.

Stomadaeum: Invagination begins.

Measurements of the embryo from the tip of the head to the posteriormost point of the yolk mass along the neural rod gave a range from 1.0 to 1.1 millimeters when the head was just beginning to form and 1.3 to 1.4 millimeters when the head was fully formed and elevated from the yolk mass. Although sections show that some somites have formed, they are not discernible externally.

The blastopore is below the posteriormost point of the neural rod and faces directly ventral during the initial period of this stage. When the head is fully formed, the blastopore faces anteriorly along the ventral surface toward the head.

Histological examination proves that the neural rod forms its neurocoel over the presumptive pharynx only. By this time the neural rod extends along approximately 75 percent of the periphery of the embryo (fig. 19). The rod is prominent and extends from the head to the blastopore.

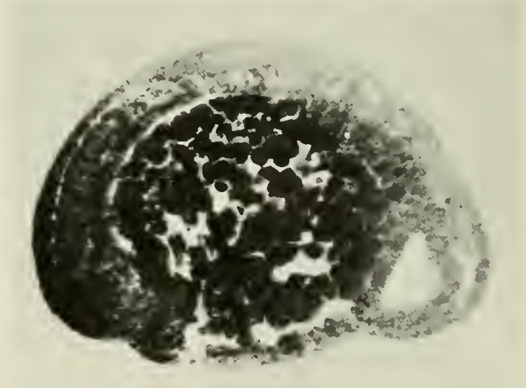

Figure 19.—Parasagittal section of stage 12.

Elongation takes place faster in the head region than in the tail region. The anterior part becomes well elevated and protrudes between the lateral swellings. The length of the head and the presumptive branchial region is about 1.0 millimeter at the end of the head stage. The appearance of a head on the exterior of the embryo marks the beginning of stage 12. This change is caused by the sudden increase in length of the neural rod during stage 11 and the sudden expansion of the presumptive pharyngeal cavity both dorsally and laterally to produce an upswelling of the prospective head from its original position.

The yolk mass retains the globular shape it had in the preceding stage. The stomodaeal invagination begins in the ventral portion between the lateral swellings.

The end-point of this stage is reached when the head region begins muscular activity.

Stage 13: Prehatching (fig. 20) days 8-12

Size: 1.4 to 2.5 millimeters.

Blastopore: Circular. Much reduced. Located at anteriormost point of apparent migration.

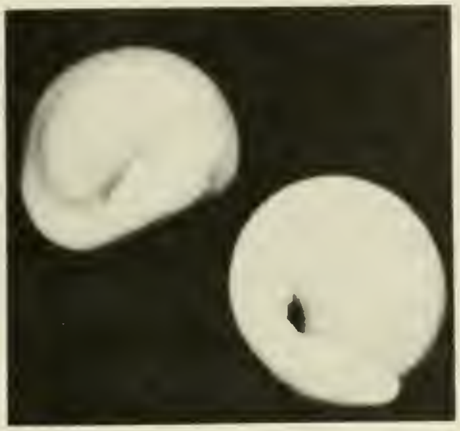

Figure 20.—Lateral view of stage 13, prehatching.

Neural tissue: Neural rod now a true neural tube. Prominent above somites from blastopore to head.

Head: 2.0 millimeters.

Yolk: Obovate, blunt end posterior.

Stomodaeum: Deepens and widens.

Somites: 5 to 20; not easily distinguished externally.

Locomotion: First muscular activity. Movement of free embryo, head.

The length of the head region has increased from 1.0 millimeter at the beginning to 2.0 millimeters at the end of this stage. Measurements were taken from the tip of the head to the anteriormost part of the yolk mass.

The blastopore, which is situated anteroventrally lies at its anteriormost position directly opposite the stomodaeal invagination.

Stage 13 begins with the advent of muscular activity. These movements initially are mere lateral flexions of the head and "neck" portion of the embryo; up-and-down activity is not apparent. As the embryo enlarges, muscular contraction includes dorsoventral flexion and becomes undulating rather than wagging. With increase in the embryo's size the perivitelline space becomes fully occupied, since the embryo, arranged in circular fashion within the membrane, begins to spiral upon itself. During this growth the above-mentioned movements become more forceful and more frequent.

Embryos that show movement but still have intact fertilization membranes are in stage 13. The endpoint of stage 13 comes when the head protrudes through the fertilization membrane to initiate hatching.

Stage 14: Hatching (fig. 21) days 10-13

Size: 3.0 to 5.0 millimeters.

Blastopore: Minute opening at apex of 90° ventral flexion of posterior. Dubious structure for staging.

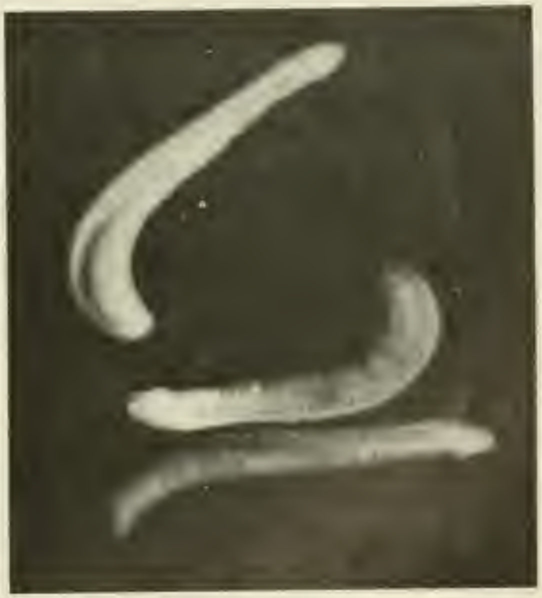

Figure 21.—Lateral view of several prolarvae of stage 14, hatching, showing posterior curvature, somites, yolk mass, and condition of mouth and nostril.

Neural tissue: Neural tube still very prominent above somites.

Yolk (gut): Becomes slender and assumes a spatulate shape. Posterior region has 90° ventral flexion. Anteriormost portion greenish.

Stomodaeum: Deep pit located ventrally.

Somites: 18–20 to 30–35. Extend from neural tube to gut.

Locomotion: Hatching movements. Undulation of anterior body region only.

Nostril: Begins as single invagination in midventral line, anterior to the stomodaeum.

Transparency: First appearance of ectodermal transparency over pericardium. Extends posteriorly and anteriorly in later phases of this stage.

Circulatory system: Pericardium visible through transparent ectoderm. Straight tubular heart. Begins beating 40 times per minute.

Liver: First indication posterior to pericardium in anterior part of gut. Appears in late period of stage.

Stage 14 starts when the embryo breaks through the fertilization membrane. The constant movement observed in stage 13 finally becomes sufficiently strong to extrude the head through the membrane. Further activity enlarges the tear in the membrane and eventually leads to hatching.

The pericardial cavity appears as a ventral swelling approximately 1.0 millimeter posterior to the tip of the head. It is also present in late stage 13 but is not easily recognized in most embryos. Shortly after hatching the ectoderm overlying the pericardial region and the tissue beneath gradually become transparent. A short time later, the body anterior to the pericardial cavity becomes transparent.

Through these transparent tissues can be seen the straight tubular heart which begins to pulsate during the eleventh day at 40 beats per minute (at 65° F.). There is no sign of blood in the heart or anywhere in the prolarva.

The end-point of stage 14 is reached when melanophores appear on the embryo.

Stage 15: Pigmentation (fig. 22) days 13-16

Size: 5 to 6 millimeters.

Neural tissue: Brain and tube visible through ectoderm.

Gut: Spatulate, changing to cylindrical. Ventral flexion of about 10° remains. Anterior face greenish.

Stomodaeum (mouth): Transverse slit bounded by thickened lips. Opens into oral cavity.

Somites: 35 to 50.

Locomotion: Undulation of entire body slightly restricted by yolk-filled gut in early stage. Full swimming movements in late period.

Nostril: Single, median at anteriormost point on ventral surface.

Transparency: Extends anteriorly to branchial region and posteriorly to about two-thirds the length of the prolarva.

Circulatory system: Heart becomes S-shaped. Heart walls thicken. Grayish channel forms in midventral gut and turns red as hemoglobin appears. Bilateral channels appear in 15th day. Heart beat, 100 per minute.

Liver: Becomes larger and vascularized.

Pigmentation: First appears as bilateral melanophores dorsal to the midbrain.

The stomodaeal pit has become a slit opening into the anterior (oral) chamber of the pharynx which is separated from the posterior (pharyngeal) chamber by the velum. The transverse slit is bounded by a thickened ectodermal lip anteriorly and posteriorly. The pharynx has its full complement of 7 visceral pouches.

Deftness of swimming increases as the shape of the yolk mass changes from spatulate to cylindrical. At the same time the tail straightens from its ventral flexion. The prolarvae progress from the awkward movements of stage 14 to an undulating movement, the smoothness of which depends on the amount of the ventral flexion of the tail.

The heart has enlarged and assumes an S-shape

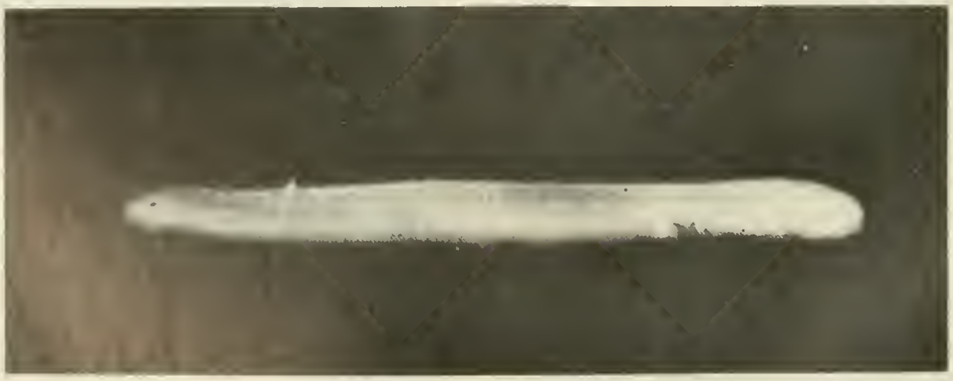

FIGURE 22.—Lateral view of stage 15, pigmentation, showing somites, pericardial area, and condition of yolk.

as the auricle moves dorsal to the ventricle. Both auricular and ventricular walls begin to thicken but remain transparent. The rate of heartbeat increases from the 40 per minute of stage 14 to 100 per minute at the end of stage 15.

Between the 13th and the 14th days a grayish channel develops along the midventral line of the cylindrical yolk mass. The channel extends from the anterior portion to the midpoint of the yolk-filled gut and within a short time turns red as hemoglobin is produced. During the 15th day bilateral channels appear along the midlateral line of the yolk mass and then converge to form a single vessel to the heart.

Stage 15 is initiated by the appearance of a pair of dorsal melanophores bilateral to the midbrain. Second and third pairs appear in sequence immediately posterior to the original ones. Shortly after the appearance of the third pair, a melanophore can be seen above the anterior branchial region. Pigmentation spreads anteriorly and posteriorly from the dorsal pairs along the neural tube (fig. 23); it spreads posteriorly and ventrally from the lateral pair along the line between the yolk and the somites, as far as the anterior limit of opaque or undifferentiated tissue. As transparency progresses, the posterior distribution of melanophores is extended correspondingly.

The end-point of stage 15 is reached with the appearance of the gill slits.

Stage 16: Gill-cleft (fig. 24) days 15-17

Size: 6 to 7.5 millimeters.

Neural tissue: Divisions of central nervous system recognized through ectoderm.

Gut: Cylindrical yolk mass. Increases in length and becomes more slender. No ventral flexion. Anterior portion greenish. Postanal gut present. Anus forms at persistent blastopore.

Mouth: Semicircular slit. Enlarges to hooded mouth. Oral cirri make first appearance.

Somites: No longer useful as staging criterion.

Locomotion: Larval swimming pattern. Very adept at end of stage.

Nostril: Migrates from anteroventral to anterodorsal extremity.

Transparency: Practically entire prolarva becomes transparent except gut.

Circulatory system: Ventricular wall has thickened. Heart beat, 150 per minute. Flow of blood readily visible.

Liver: Size increases. Distinctly separated from gut.

Pigmentation: Melanophores extend along dorsum and sides of embryo from anterior to posterior. Bilateral eyespots appear at end of stage.

Gill clefts: First appearance. They become functional.

Respiratory rate: 120 per minute.

Fins: Caudal and anal fins appear.

The mouth continues to migrate anteriorly and

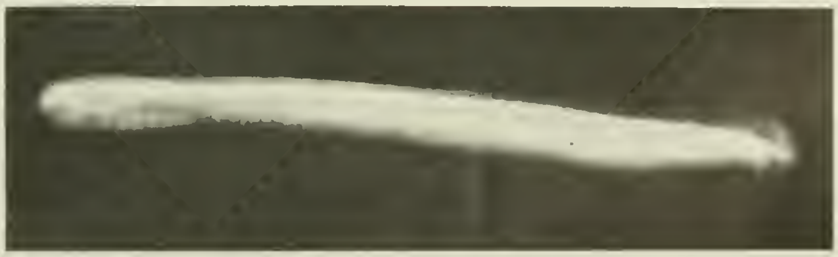

FIGURE 23.—Dorsal view of stage 15 showing condition of pigmentation over the head region.

FIGURE 24.—Lateral view of stage 16, gill cleft, showing gill clefts, somites, pericardial area, and pigmentation over yolk mass.

the nostril dorsally. The anterior lip of the slit-like mouth of stage 15 moves anteriorly at the midline only, producing a semicircular mouth. Migration of the anterior lip and nostril continues until the mouth lies at the anteroventral extremity and the nostril is at the anterodorsal extremity. In later phases of the stage the mouth enlarges and is hooded by the anterior lip. Oral cirri begin to form posterior to the anterior and posterior lips.

Movement during this stage is by a rapid undulation of the trunk and tail. All ventral flexion of the tail region has disappeared during the transition from stage 15 to 16.

The anterior boundary of the auricle lies over the center of the ventricle. The flow of blood through the heart and other parts of the prolarva is seen readily.

In the latter period of this stage the bilateral pigmented retina (eyespot) appears anterior and dorsal to the velum. Melanophores which extend down the length of the neural tube and along the yolk-filled gut begin to migrate ventrally from both levels. Melanophores migrate along the myosepta from the neural-tube level and ventrally from the yolk-somite line. The anterior lip and head region also are well pigmented.

The appearance of gill clefts marks the initiation of stage 16. They appear and start functioning in order from the first to the seventh. Functioning of the branchial apparatus can be determined by two means: beating of the velum (between the oral cavity and the first visceral cleft) as it forces water through the pharynx; or, contractions of the gill clefts. The respiratory rate (velum beat) is 120 per minute.

The end-point of stage 16 is reached when the prolarvae acquire bilateral eyespots and are about to burrow.

Stage 17: Burrowing (fig. 25) days 17-33

Size: 7.5 to 9.0 millimeters.

Gut: Cylindrical and yolk-filled. Postanal gut absorbed. Esophagus visible on left side. Cloaca transparent. Peristaltic movements in hind gut. Lumen of gut opens at end of stage.

Mouth: Oval with dorsal and ventral lips. Opens anteriorly. Oral cirri.

Locomotion: Swimming movements same as in stage 16. Prolarvae burrow.

Nostril: On dorsal aspect, its ultimate position.

Transparency: Complete except for yolk-filled gut.

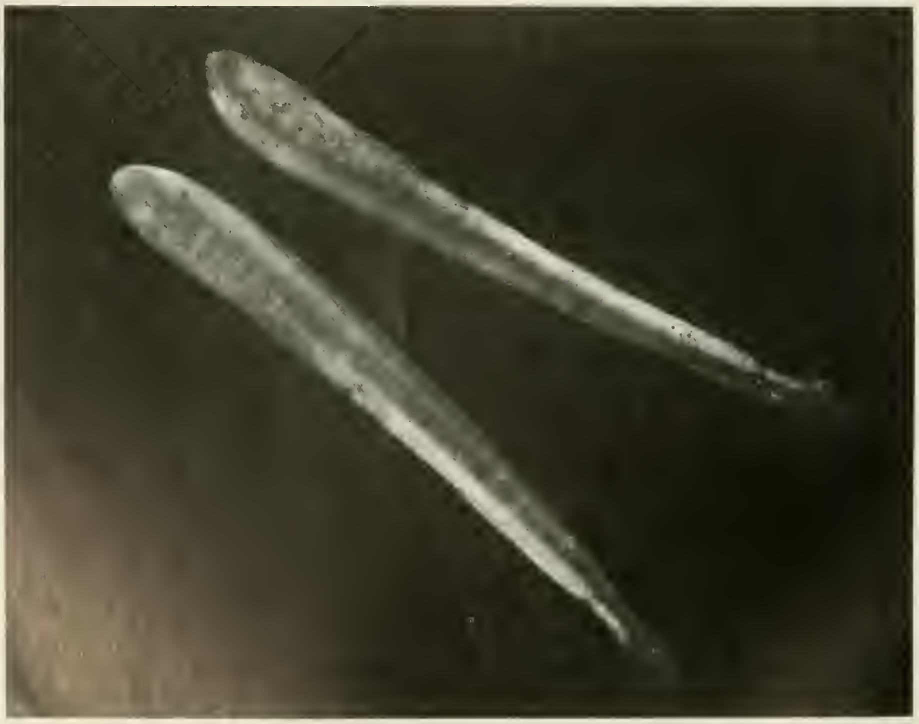

Figure 25.—Lateral views of stage 17, burrowing, showing the condition of the mouth and the lips.

Circulatory system: Heart walls thicken. Heart beat more than 200 per minute. Flow of blood visually traceable throughout most of prolarva.

Liver: Further increases in size. First indication of gall bladder on right side.

Pigmentation: Melanophores extensively distributed. Aggregation over pronephric region and caudal end of notochord and neural tube.

Respiratory rate: 200 per minute.

Pronephros: First detectable externally.

The posterior region of the gut becomes transparent as the cloaca is formed with the opening of the pronephric ducts into the gut (histological observations). A yolk pellet forms in the gut anterior to the cloaca as the result of peristaltic movements of the gut. These movements move the pellet toward the anus and then back to the remaining yolk mass.

The lips take on the characteristic larval form. The mouth opens directly anteriorly, so that the anterior lip has now become the dorsal lip and the posterior lip the ventral.

Stage 17 begins when the prolarvae burrow into the bottom mud. Burrowing is the result of the action of both the tail and the head regions. As the head moves from side to side to create space within the mud, the lashing of the tail drives the prolarva into the mud. Prolarvae of this stage placed in aquaria or beakers first swim near the surface of the water and then suddenly plunge downward with rapid swimming movements until they reach the bottom, when they immediately begin to burrow. Prolarvae of stage 16 merely drift down to and lie on the bottom. Swimming movements do not differ from those of stage 16.

The liver is extended farther and the presence of the gall bladder in the later period is marked by its bile-green color.

The eyespot or retina is very prominent anterior and dorsal to the velum. Melanophores have spread completely around the gut region to the ventral surface. They have migrated down the lateral surface of the velum and the gill bars, and have completely outlined the branchial basket. The dorsal lip is covered completely with melanophores.

A pronephros dorsal and posterior to either side of the pericardial cavity is visible externally because of the presence of much blood. This stage is the first in which the pronephros is visible externally.

The end-point of stage 17 is reached when the lumen of the yolk-filled gut is opened.

Stage 18: Larva (fig. 26) days 33-40

Size: 9 millimeters and longer.

Gut: Lumen completely opened. Yolk extruded from gut. Gut tissue becomes transparent.

Respiratory rate: 200 per minute.

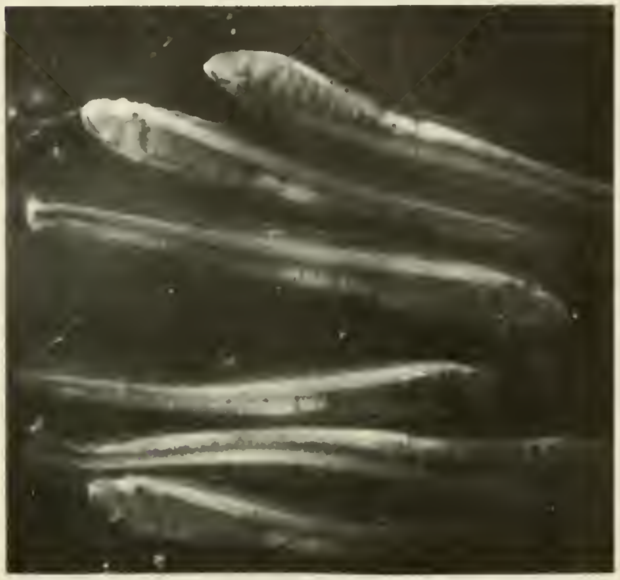

Figure 26.—Various views of several stage 18 larvae on a black background. Shown are: condition of the mouth and lips, eyespot, pigment outlining branchial region, liver immediately posterior to the heart, somites, fins, and the gut from the liver to the cloaca. The granular appearance along the gut is caused by pigmentation.

The transition from the prolarval to the larval condition (all systems differentiated save genital) is marked by the differentiation of the formerly yolk-filled gut into its definitive form. This change is seen outwardly as the gut becomes transparent at the "stomach" region behind the liver. Transparency progresses posteriorly until the entire gut has differentiated and the digestive system is open from the mouth to the anus. After the pellet described in stage 17 is passed, yolk remaining within the lumen of the gut is extruded constantly from the anus.

Stage 18 larvae are between 9 and 10 millimeters long at the time the gut becomes fully differentiated. They belong to the first larval stage which would be equivalent to age-group 0, 11 to 21 millimeters long, of Applegate (1950).

REVIEW OF STAGES AND COMPARISON WITH EARLIER STUDIES

Staging of lampreys in most early literature lacked precision. Investigators, for example, Shipley 1885, Scott 1887, McClure 1893, Hatta 1914, 1915, who studied early embryology, gave little or no attention to the need for staging. Developmental sequence was described in conventional embryological terms.

The first serious attempt to show stages of lamprey development was by Damas (1944) in his excellent histological study of *L. fluviatilis*, concerned primarily with tracing development of the head. Each section (comparable to a stage) comprised a short account of external features and a thorough histological description. His staging series began with embryos possessing 3 somites (section 1). The next section included embryos with 10 somites. (Every somite listed by Damas was not visible in external view, but each was seen histologically.) On the basis of somite numbers Damas was able to describe several stages slightly different from each other which could be described also by staging based on external morphological features. Some of his sections, based usually on intervals of 10 somites, have been translated into stages of the present study for comparison in table 1.

Stages described in the present work have been based primarily on changes of external features. Histological observations have been used sparingly and merely for clarification. Damas, who began his study after development had started, omitted the first 9 stages of the present work. Because his criteria were histological, his stages are overlapped by stages in the present study (table 1).

TABLE 1.—*Equating of "sections" of Damas (1944) study with "stages" of the present research*

Damas (section)	I	II	III	IV	V
Piavis (stage)	10	11	12	12	13
Damas (section)	VI	VII	VIII	IX	X
Piavis (stage)	13	13	14	14	14
Damas (section)	XI	XII	XIII	XIV	XV
Piavis (stage)	15	15	15	16	18

Staging, to be of practical value, should be simply, easily, and promptly recognized by investigators in both living and preserved materials. By far the easiest method of designating stages is one based on morphological characteristics since the resulting demarcations are relatively sharp and distinct and the diagnostic features are visible without elaborate histological preparation. They are natural divisions in a developmental sequence. Particular effort was made in this study to avoid dependence on measurements and counts. Ideally, observation alone should suffice for recognition of stages.

Applegate (1950) divided the larval forms of *P. marinus* on the basis of length and weight into age groups, beginning with age-group 0. He stated that the larvae ". . . upon leaving the nest have completed their early developmental stages and are perfectly formed but diminutive ammocoetes." These ammocoetes are in reality stage 18 larvae, for specimens from Applegate's collections match specimens from my collections in their external as well as histologic characteristics.

Stages, as designated here, can be determined by the naked eye or with a hand lens. Separation of stages 12 and 13 might conceivably cause some difficulty since transition between them is based on muscular activity. It is easy, however, to recognize preserved specimens, for the head region of embryos of stage 13 is displaced to either side of midline whereas heads of stage 12 embryos are medial.

Cleavage in the sea lamprey has several interesting characteristics, the first of which is the appearance of relatively high prominences lateral to and above the first cleavage furrow. Similar prominences occur during second cleavage (stage 3).

McClure (1893) noted the unusual cleavage pattern of *P. marinus*, especially in the third and fourth cleavages. He described the third cleavage as meridional and considered this to be the sole type of third cleavage. Actually, both meridional and equatorial types of third cleavage occur, but their relative abundance fluctuated widely irrespective of temperature.

Teleostei, Gymnophiona, Gallus, and other forms exhibit a meridional third cleavage, which, however, is accomplished in meroblastic division. In the sea lamprey the meridional third cleavage is holoblastic.

The cleavage of stage 4 embryos determines the type of cleavage for stage 5, since an equatorial stage 4 is followed by meridional stage 5 and vice versa.

Cleavage of stage 6 embryos is indeterminable and is accompanied by a lag in the cleavage of the vegetal cells. After stage 6, demarcation between the animal and vegetal cells is sharp until the vegetal cells are covered by the epibolizing animal cells.

Blastopore formation, as was observed by Shipley (1885), involves behavior of animal cells and vegetal cells similar to that in amphibians and teleosts. When invagination of animal cells forms the blastopore, the margin of animal cells is arranged latitudinally around the embryo from the blastopore. As the animal cells continue to epibolize, the vegetal cells are covered by animal cells from the anterior and dorsolateral portions of the animal hemisphere and subsequently from the posterolateral and ventral positions in the fashion described for stage 9. Thus, migration of animal cells over vegetal cells in the lamprey matches closely the epiboly of animal cells in amphibians. The dorsal lip does not curve as much, however, in the sea lamprey as in amphibians. If the blastopore is considered to be defined by the line of epibolizing animal cells, as it is in teleosts, the blastopore of the sea lamprey is at first oval. This shape results from alignment of animal cells lateral to the midsagittal plane. A circular blastopore is formed when animal cells at the ventralmost point of the oval-shaped blastopore cover the oval yolk plug in a ventral-to-dorsal direction along the mid-sagittal plane.

The circular blastopore of the sea lamprey apparently migrates toward the center of the animal hemisphere whereas the teleost blastopore migrates toward the vegetative pole as the embryo lengthens. The amphibian blastopore eventually reaches and passes beyond the vegetative pole at a stage equivalent to stage 13 of the lamprey. Because teleost embryos do not extend ventrally over the yolk mass the blastopore does not reach the vegetative pole.

The apparent migration of the lamprey blastopore might possibly be attributed to the decrease in the volume of the blastocoel during stages 9 and 10. An increase in embryo volume which takes place in stage 8 is apparently due primarily to the increased volume of the blastocoel. During stage 9, after involution is completed, the volume of the embryo decreases as the result of a decrease in the volume of the archenteron. The archenteron, in reality, is the original blastocoel since the blastocoel is not obliterated during gastrulation (histological observations) as it is in amphibians. In this feature of gastrulation the lamprey closely resembles teleosts. Since decrease in the size of the archenteron shortens the embryo and since growth of the neural tube in stages 12 and 13 moves the blastopore along the mid-sagittal plane, the blastopore appears to migrate.

The present study also corroborates Shipley's (1885) observation that the open blastopore persists, eventually becoming the anus. Histological sections permit tracing the archenteron to an open blastopore through stage 15. During stage 16, the diameter of the blastopore widens and the lips thicken to form the anus. The archenteron can be traced to the anus in stage 16 as it was traced to the blastopore in stage 15.

Shipley recognized that the early neural tube did not possess a neurocoel and called it a neural rod, which term has been retained here. Selys-Longchamp (1910) described neural-tube formation in lampreys as intermediate between the keel method of teleosts and neural-fold method of other vertebrates.

Among the morphological features prominent during development were the gut, liver, gall bladder, hemoglobin and vascularization, and pigment. The gut opens from the oral cavity to the anus at stage 18. The stomodaeum opens in stage 16, the esophagus in stage 17, the cloaca in stage 17, and finally the portion between esophagus and cloaca at stage 18.

The formation of the liver in late stage 14 is indicated by the greenish cast of the anteriormost portion of the gut. Vascularization of the liver occurs during stage 15. The size of the liver continues to increase through stages 15 and 16. A gall bladder forms in stage 17; it is recognizable externally by its accumulation of blue-green bile.

Additional changes in stage 15 embryos include the appearance of hemoglobin within the blood channels which had formed in the yolk-filled gut. Blood cells appear first in the midventral channel and soon are in all three major channels. Blood formation and the bulk of vascularization take place in stages 15 and 16. Vascularization is extended in stage 17, when practically all major vessels can be traced by following red corpuscles within the transparent tissues.

Pigmentation of the embryo begins as two melanophores bilateral to the midbrain. Successive pairs of melanophores appear posterior to the initial one; next is the appearance of a melanophore above the branchial region. The number of melanophores increases throughout stage 15 when they loosely cover the dorsum and form a line posteriorly from the branchial region between yolk and somites. In stage 16 melanophores extend along the dorsum and sides of the embryo. Bilateral eyespots appear at the end of stage 16. The melanophores become more extensively distributed in stage 17. Aggregations appear over the pronephric region and the caudal end of the notochord and neural tube. The anterior lip, and the head region and the gut become profusely covered with pigmentation. The pattern of pigmentation changes little in stage 18 except that the pigmented area is extended.

Activity in the embryo included locomotory movements, heart beat, and velum beat. First evidence of activity is the movement of the head region, produced by muscles of somites of stage 13 embryos. Greater muscular movements take place during later stages, including the movements that lead to: hatching; poor swimming movements of stage 14; somewhat better swimming in stage 15; the greatly increased deftness of swimming in stage 16; and movements which accomplish burrowing at stage 17.

Changes in the heart region in stage 14 embryos can be seen through the ectoderm over the pericardial cavity as it becomes transparent. The heart begins to beat at a rate of 40 times per minute, increasing to 100 per minute in stage 15, 150 per minute in stage 16, and more than 200 per minute in stage 17.

The respiratory system becomes functional at stage 16 when the initial respiratory rate (velum beat) is 120 per minute. This rate increases to 200 per minute in stage 17 and is maintained at this rate into stage 18.

In general, lamprey development resembles amphibian development in cleavage (stages 1–8). Lamprey gastrulation resembles amphibian gastrulation in some respects and teleostean in others. Epiboly is more like that of amphibians than of teleosteans. Invagination and involution of chorda-mesoderm seem similar to that in amphibians. Formation of the lamprey archenteron produces a situation comparable to that of a teleost. In both, the developing embryo is located on a large yolk mass but separated from the yolk by an archenteron which was the original blastocoel. A major difference between the two is that lamprey yolk is divided whereas teleostean yolk remains undivided. Another similarity to teleostean development is the formation of a solid neural rod which develops a lumen only after neurulation has been completed.

DEVELOPMENT AT DIFFERENT CONSTANT TEMPERATURES

The primary objective of the experimental rearing of sea lampreys at a series of constant temperatures was to determine the temperature levels at which the eggs were capable of developing into normal, viable larvae. As part of the work, detailed records were kept on: the relation between temperature and progression of development; mortality rate during development; occurrence and nature of developmental abnormalities. Information of this type may help explain the failure, noted both in the United States and in Canada, of the sea lamprey to utilize certain apparently suitable spawning streams as extensively as other apparently similar waters.

MATERIALS AND METHODS

The experiments were conducted at temperatures and with the aid of equipment indicated in table 2. Throughout this work, control lots at 65° F. were maintained as an index to development. Thus, any one control lot could serve effectively as an indicator to several other experiments. Eggs from 2 to 4 females were mixed with sperm from 4 to 8 males. These eggs were then apportioned into containers in the numbers (by actual count) indicated in table 3.

Table 2.—*Equipment used in experiments on development at constant temperatures*

Temperature (° F.)	Temperature-control equipment	Temperature (° F.)	Temperature-control equipment
45	Refrigeration.	65	Heat, refrigeration (Bronwil circulator).
50	Refrigeration.	70	Heat.
52.5	Refrigeration.	75	Circulator.
55	Refrigeration.	77.5	Circulator.
60	Heat and refrigeration.	80	Circulator.

The sampling schedule differed somewhat among the experiments (as may be seen from later tables that give details for individual samples) but the differences of schedule and the unavoidable occasional interruptions of timing were not sufficient to impair comparisons between series or to hamper the description of the progress of development. In the main, the earlier samples were taken at 1- or 2-hour intervals; the time between samples

Table 3.—*Specimens and number of eggs used in experiments on development at constant temperatures*

[One group of lampreys provided the eggs for experiments conducted at 45°, 55°, 70°, 75°, and 80° and another group for those at 52.5°, 60°, and 77.5°. Eggs from the lots that supplied materials for experiments at 50° and 65° were reared at the one temperature only]

Water temperature (° F.)	Number of females	Number of males	Number of eggs
45	4	8	10,000
50	2	4	10,000
52.5	2	4	15,000
55	4	8	25,600
60	2	4	9,000
65	2	4	33,000
70	4	8	18,000
75	4	8	13,500
77.5	2	4	9,000
80	4	8	5,000

was increased to 4 hours at about 32 hours; later samples (that is, after 2–3 days) were obtained about 12 hours apart; and, finally in the longer experiments sampling was daily. Sampling after stage 14 appeared was biased because the prolarvae had to be pursued as they became older; thus the samples were non-representative in comparison with the random samples for all earlier stages. In the main the bias led to over-representation of live specimens.

Several criteria were used to separate live and dead embryos. The most obvious indication of death was disintegration of the embryo—a separation of cells and subsequent filling of the intramembrane volume with loosely arranged cells, within an intact membrane. Furthermore, the fertilization membrane became translucent with a cloudy cast in contrast to the transparency of a living membrane. This difference was most apparent in later development, stages 7–14; the earlier stages (1–6) became vacuolated as they underwent changes after death. Eventually, the membranes of eggs in these earlier stages also became cloudy. Another indicator, particularly in early development, was a change of color from the creamy white of normal eggs to a brownish tan, accompanied by a fuzzy appearance of the surface. Dying embryos of stages 9–11 possessed appreciably widened blastopores, which in some extended across the entire diameter of the embryo.

The basic data on the several temperature experiments are given in the records of number of dead embryos and number of living embryos in various stages of development. In conjunction with these records, information was recorded relative to the elapsed time and temperature and remarks were noted concerning the general composition of each sample.

The percentage of dead embryos was computed for each sample. Until stage 14 appeared this percentage provided an estimate of mortality up to the time of sampling since all embryos regardless of time of death were included in the computations. This procedure was possible since all eggs used in any one experiment were recoverable throughout the experiment. Although disintegration of dead embryos did occur, the embryonic membrane remained intact to the end of the experiment. The information on dead embryos per sample does not include data on time of death, since stages could not be determined for embryos that were decomposing, but it does provide good information on the progression of mortality with development.

Because, as has been stated, the quantitative sampling of lots of eggs become biased after the appearance of stage 14 (hatching) and later stages, none of the tables that carry details on individual samples goes beyond the last sample that contained stage 13 embryos (the bias starts, of course, with the first sample containing stage 14 specimens, but full records for stage 13 appear to be desirable). In the experiments in which stage 14 was not reached, the tabulation ends with the last sample that contained live embryos. Similarly, the tables showing mortality by 1-day intervals end with the records for the first day on which stage 14 appeared, or, if that stage was not reached, with the last day on which samples contained live embryos. Terminal samples are included for those experiments in which some embryos survived the full term of the experiment or in which there was cause to suspect that a few live embryos might still be present. These terminal samples which contained all eggs remaining at the end of the experiment are considered, for practical purposes to be unbiased. They were affected to some degree by the earlier removal (after the start of stage 14) of samples in which living embryos were taken out of proportion to their true abundance, but the numbers were so much greater in the terminal sample than in these earlier biased samples as to minimize the distorting effect.

Records from biased samples were of course useful for showing the time of first appearance and duration of the later stages.

ACCOUNT OF INDIVIDUAL EXPERIMENTS

Development at 45° F.

The sea lamprey eggs could not make even a good start toward development in a constant temperature of 45° F. The first two cleavages (stages 1 and 2) proceeded very slowly and all eggs were dead before the third cleavage was completed (tables 4 and 5; fig. 27).

TABLE 4.—*Living and dead lamprey embryos per sample and their stage of development at 45° F. (7.2° C.)*

Sample	Number of hours	Number dead	Stage of living embryos		
			1	2	3
1	1	67	213	-----	----
2	3	15	105	-----	----
3	5	10	94	-----	----
4	7	13	125	-----	----
5	9	16	169	-----	----
6	11	17	120	-----	----
7	13	11	113	-----	----
8	15	73	92	-----	----
9	17	38	233	-----	----
10	19	82	84	33	----
11	21	45	76	109	----
12	23	45	-----	101	----
13	25	62	-----	63	----
14	27	91	----	23	----
15	31	105	----	57	----
16	35	120	----	23	----
17	39	123	----	32	----
18	43	85	----	16	----
19	47	177	----	22	2
20	51	207	----	8	4
21	58	175	----	-----	10
22	71	252	----	-----	14
23	82	322	----	-----	3
24	95	363	----	-----	2
25	103	341	----	-----	2

TABLE 5.—*Mortalities of sea lamprey eggs reared at a constant temperature of 45° F. (7.2° C.)*

Time		Stage span	Number of samples	Number of embryos			Percentage dead
Hours	Days			Alive	Dead	Total	
0–24	1	0–2	12	1,667	432	2,099	21
25–48	2	2–3	7	238	763	1,001	76
49–72	3	2–3	3	36	634	670	95
73–96	4	3	2	5	685	690	99
97–120	5	3	2	2	579	581	[1] 100

[1] More than 99.5; actually all embryos (238 specimens) were dead in the sample taken at 116 hours.

Stage 1 lasted about 20 hours; stage 2 commenced at the 19th hour and lasted beyond the 47th hour, when a highly defective stage 3 appeared (tables 4 and 6; fig. 28). Many 3-cell embryos were found along with a few abortive 4-cell embryos, in which the cleavage furrow seemed to undergo regression.

Throughout the samples, beginning with the sixth at 11 hours, the eggs began to vacuolate and to fragment yolk into the perivitelline space, in short, to die and disintegrate. Beginning with the 19th sample, at 47 hours nearly 90 percent

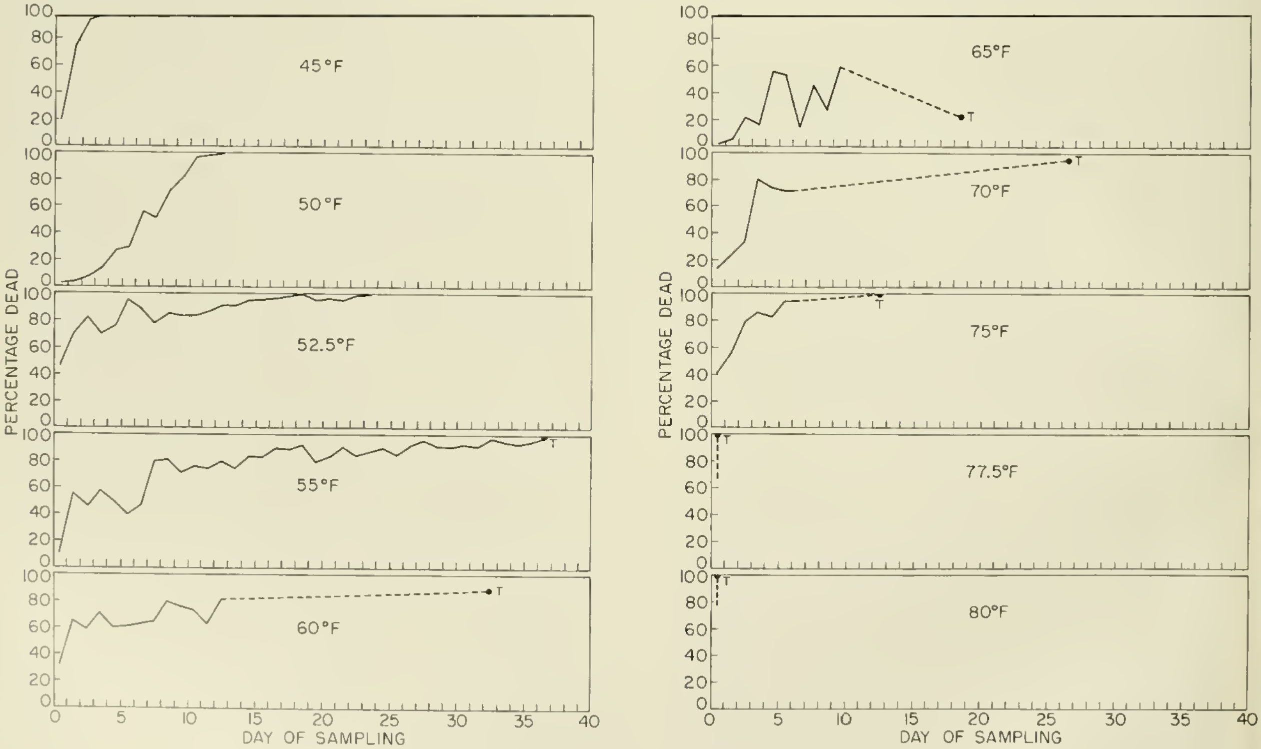

FIGURE 27.—Percentage of dead embryos in daily samples from sea lamprey eggs reared at 10 different constant temperature levels. The day-by-day records end when the percentage of dead in the samples reached and remained at 100, or with the onset of hatching. A broken line connects the last recorded daily sample with the terminal sample (T). At 77.5° and 80° live embryos occurred in the earlier samples of the first day but none in the later ones.

TABLE 6.—*Hours at which the first and last specimens of the various stages appeared in samples during each experiment and the duration of stages (in parentheses)*

Stages	Constant temperature (F.) at which embryos were reared									
	45°	50°	52.5°	55°	60°	65°	70°	75°	77.5°	80°
1	1-21 (21)	1-16 (16)	1-10 (10)	1-13 (13)	1-6 (6)	1-2 (2)	1-3 (3)	1-3 (3)	1-4 (4)	1-7 (7)
2	19-51 (33)	6-25 (20)	3-22 (20)	3-23 (21)	3-10 (8)	2-8 (7)	5-7 (3)	5 (2)	4-6 (3)	5-9 (5)
3	47-103 (57)	19-34 (16)	13-28 (16)	15-31 (17)	13-16 (4)	8-11 (4)	7-11 (5)	7 (2)	6-10 (5)	9-11 (3)
4		28-42 (15)	20-36 (17)	23-35 (13)	16-18 (3)	10-15 (6)	11-13 (3)	7-11 (5)	10 (4)	([3])
5		34-48 (15)	32-44 (13)	31-43 (13)	20-22 (3)	13-15 (3)	13-15 (3)	9-13 (5)	[2] 13	([3])
6		40-58 (19)	40-48 (9)	39-47 (9)	22-28 (7)	16-19 (4)	15-17 (3)	13-15 (3)	[2] 13	[2] 15
7		44-78 (35)	48-64 (17)	47-103 (57)	28-34 (5)	19-24 (6)	17-21 (5)	15-17 (3)		
8		62-126 (65)	68-136 (69)	51-151 (101)	36-89 (54)	28-64 (37)	19-51 (33)	19-43 (25)		
9		114-270 (167)	160-338 (179)	127-271 (145)	100-148 (49)	64-104 (41)	47-82 (36)	43-82 (40)		
10			338-362 (25)	211-295 (185)	136-172 (37)	104-128 (25)	82-103 (22)	71-103 (33)		
11			362-470 (109)	295-405 (111)	172-220 (49)	128-152 (25)	103-127 (25)	95-116 (22)		
12			470-570 (101)	369-525 (157)	208-283 (76)	152-200 (49)	116-151 (36)	103-139 (37)		
13				[1] 490-874 [4] (--------)	283-409 (127)	200-296 (97)	151-235 (85)	151-175 (25)		
14					317-409 (93)	[4] 248- [4] (--------)	175-247 (73)	175-211 (37)		
15					352-469 (118)	[4] 308- [4] (--------)	225-307 (83)	211-225 (15)		
16					446-569 (124)	[4] 363- [4] (--------)	295-343 (49)	[1] 225-307 [4] (--------)		
17					[1] 594-782 [4] (--------)	[1] 405-437 [4] (--------)	[1] 357-633 [4] (--------)			

[1] Termination of experiment.
[2] 100-percent mortality subsequent to this hour.
[3] No embryo of this stage found in any sample.
[4] These blanks cannot he filled properly for these stages were sampled either in or immediately preceding the terminal sample.

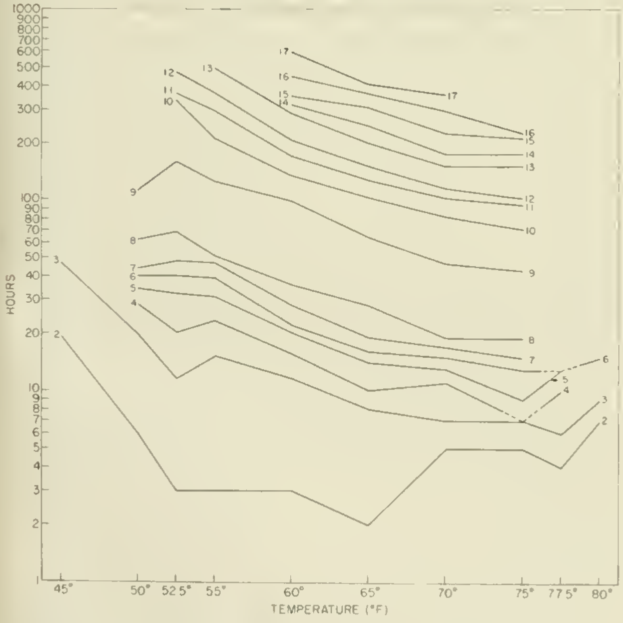

FIGURE 28.—Number of hours required by sea lamprey embryos to reach different developmental stages when reared at various constant temperatures.

of the eggs were dead. All eggs obviously were dead in samples taken after the 5th day (table 5). Eggs marked by lesions as described by Damas (1948) did not undergo first cleavage.

The highest stage completed in this experiment was stage 2, since stage 3 was not consummated.

Development at 50° F.

The rate of development was decidedly faster at 50° F. than at 45° F. (table 6; fig. 28) and development proceeded farther. Stage 9 was reached but few embryos survived to the end of the stage (tables 7 and 8; fig. 27). A single sample contained eggs that seemed to be intermediate between stages 9 and 10. No embryos were alive after the 270 hours (sample 65, table 7; table 6, also fig. 27).

The duration of each of the first 6 stages fell within the limited range of 15–20 hours (table 6). Stage 7, however, lasted 35 hours, and stage 8 approximately 65 hours, the longest save for the last stage reached (stage 9). The greatest period overlap of stages occurred between stages 7 and 8

TABLE 7.—*Living and dead embryos per sample and their stage of development at 50° F. (10° C.)*

Sample	Hours	Number dead	Stage of living embryos								
			1	2	3	4	5	6	7	8	9
1	½	-	93	-	-	-	-	-			
2	1	-	140	-	-	-	-	-			
3	2	-	215	-	-	-	-	-			
4	3	-	184	-	-	-	-	-			
5	4	-	133	-	-	-	-	-			
6	6	1	200	20	-	-	-	-			
7	7	1	157	43	-	-	-	-			
8	8	-	132	34	-	-	-	-			
9	10	1	108	30	-	-	-	-			
10	11	-	129	18	-	-	-	-			
11	12	-	132	27	-	-	-	-			
12	13	-	112	68	-	-	-	-			
13	14	-	31	84	-	-	-	-			
14	15	-	42	139	-	-	-	-			
15	16	1	14	111	-	-	-	-			
16	17	6	-	139	-	-	-	-			
17	18	6	-	151	-	-	-	-			
18	19	8	-	283	2	-	-	-			
19	20	11	-	304	62	-	-	-			
20	21	12	-	271	127	-	-	-			
21	22	8	-	141	213	-	-	-			
22	23	10	-	72	210	-	-	-			
23	24	6	-	47	262	-	-	-			
24	25	7	-	13	95	-	-	-			
25	26	5	-	-	117	-	-	-			
26	27	4	-	-	72	-	-	-			
27	28	-	-	-	48	12	-	-			
28	29	-	-	-	50	48	-	-			
29	30	18	-	-	137	190	-	-			
30	32	23	-	-	90	344	-	-			
31	34	19	-	-	26	453	23	-			
32	36	-	-	-	-	43	60	-			
33	38	3	-	-	-	24	80	-			
34	40	3				7	60	5	-	-	-
35	42	3				5	19	89	-	-	-
36	44	17				-	69	232	8	-	-
37	46	14				-	49	187	5	-	-
38	48	10				-	8	83	30	-	-
39	50	13				-	-	108	107	-	-
40	54	25				-	-	41	163	-	-
41	58	11				-	-	17	132	-	-
42	62	15				-	-	-	87	183	-
43	66	14				-	-	-	13	125	-
44	70	13				-	-	-	11	271	-
45	74	35				-	-	-	5	335	-
46	78	71				-	-	-	2	236	-
47	90	32				-	-	-	-	238	-
48	102	87				-	-	-	-	119	-
49	114	42				-	-	-	-	209	7
50	126	32				-	-	-	-	77	12
51	137	93				-	-	-	-	-	217
52	146	43				-	-	-	-	-	57
53	150	123				-	-	-	-	-	125
54	163	119				-	-	-	-	-	41
55	171	118				-	-	-	-	-	210
56	174	207				-	-	-	-	-	135
57	182	169				-	-	-	-	-	205
58	187	232				-	-	-	-	-	134
59	198	337				-	-	-	-	-	106
60	211	315				-	-	-	-	-	123
61	222	283				-	-	-	-	-	82
62	234	254				-	-	-	-	-	25
63	246	375				-	-	-	-	-	10
64	260	435				-	-	-	-	-	2
65	270	634				-	-	-	-	-	6

TABLE 8.—*Mortalities of sea lamprey eggs reared at a constant temperature of 50° F. (10° C.)*

Time		Stage span	Number of samples	Number of embryos			Percentage dead
Hours	Days			Alive	Dead	Total	
0-24	1	0-3	23	4, 680	71	4, 751	2
25-48	2	3-7	15	2, 781	126	2, 907	4
49-72	3	6-8	6	1, 258	91	1, 349	7
73-96	4	7-8	3	816	138	954	14
97-120	5	8-9	2	335	129	464	28
121-144	6	8-9	2	306	125	431	29
145-168	7	9	3	223	285	508	56
169-192	8	9	4	684	726	1, 410	52
193-216	9	9	2	229	652	881	74
217-240	10	9	2	107	537	644	83
241-264	11	9	2	12	810	822	99
265-288	12	9	2	6	1, 222	1, 228	99. 5

(20 hours) and the next longest between stages 8 and 9 (12 hours). Mortality was light the first 3 days (2 to 7 percent dead; table 8) and was moderate (14 to 29 percent dead) the next 3 days. The death rate increased considerably shortly after the embryos entered stage 9 (gastrula). Samples on the seventh day contained 56 percent of dead eggs. The percentage had reached 99 and 99.5 percent on the 11th and 12th days, respectively, and all eggs were dead on the 13th day.

Development at 52.5° F.

Again, an increase of temperature (this time only 2.5° above that of the experiment described in the preceding section) permitted development at a faster rate and through a greater number of stages (table 6; fig. 28). Heavy mortality started early, however, the death rate increased as development progressed (tables 9 and 10; fig. 27), and no embryos survived beyond stage 12 (head stage).

The early stages (1 to 6) of this experiment proceeded slightly more rapidly than the corresponding stages of the 50° F. experiment. The periods of overlap of the earlier stages were nearly equal to those of the 50° F. test, although the length of time for each stage was less at 50° F. than at 52.5° (tables 6, 7, and 9). Stage 9 was prolonged at 52.5° F. over a period of approximately 9 days. During this time the number of deaths increased. The relatively few embryos that developed beyond stage 9 progressed through a short stage 10 and a much longer stage 11 (about 4 days). Stage 12 was reached by approximately 40 embryos, all of which died. The most frequent symptom of death was disintegration of the anterior region of the embryos.

Development at 55° F.

Development at 55° F. proceeded as far as stage 13 (prehatching). Indeed, the terminal sample included 11 live embryos in this stage (along with some 16,000 dead embryos) but all of them were so defective as to make early death almost certain; they were accordingly classed as

TABLE 9.—*Living and dead embryos per sample and their stage of development at 52.5° F. (11.4° C.)*

Sample	Hours	Number dead	Stage of living embryos											
			1	2	3	4	5	6	7	8	9	10	11	12
1	1	2	76											
2	3	11	29	2										
3	5	15	23	4										
4	6	7	76	3										
5	8	8	36	2										
6	10	21	31	1										
7	13	31		15	1									
8	14	47		23	2									
9	16	38		9	1									
10	18	74		12	3									
11	20	27		2	10	1								
12	22	37		2	12	3								
13	24	48			7	3								
14	26	33			2	10								
15	28	39			2	16								
16	32	29				13	12							
17	36	44				2	11							
18	10	49					2	10						
19	44	66					2	15						
20	48	29						4	21					
21	54	51							18					
22	64	65							5	2				
23	76	21								9				
24	89	46								20				
25	100	32								13				
26	112	72								21				
27	124	50								5				
28	136	142								6				
29	148	37												
30	160	33									10			
31	172	58									20			
32	814	57									12			
33	196	76									13			
34	281	44									12			
35	230	70									10			
36	242	65									12			
37	254	86									17			
38	269	40									6			
39	293	75									9			
40	302	78									7			
41	327	53									5			
42	338	64									4	1		
43	349	96										4		
44	362	85										2	1	
45	375	96											5	
46	386	79											2	
47	419	117											2	
48	447	44												
49	470	83											1	3
50	494	98												3
51	518	68												3
52	543	79												1
53	570	92												1

TABLE 10.—*Mortalities of sea lamprey eggs reared at a constant temperature of 52.5° F. (11.4° C.)*

Time		Stage span	Number of samples	Number of embryos			Percentage dead
Hours	Days			Alive	Dead	Total	
0–24	1	0–4	13	389	366	755	48
25–48	2	3–7	7	122	289	411	70
49–72	3	7–8	2	25	116	141	82
73–96	4	8	2	29	67	96	70
97–120	5	8	2	34	104	138	75
121–144	6	8	2	11	192	203	95
145–168	7	9	2	10	70	80	88
169–192	8	9	2	32	115	147	78
193–216	9	9	1	13	76	89	85
217–240	10	9	2	22	114	136	84
241–264	11	9	2	29	151	180	84
265–288	12	9	1	6	40	46	87
289–312	13	9	2	16	153	169	91
313–336	14	9	1	5	53	58	91
337–360	15	9–10	2	9	160	169	95
361–384	16	10–11	2	8	181	189	96
385–408	17	11	1	2	70	72	97
409–432	18	11	1	2	117	119	98
433–456	19		1		44	44	100
457–480	20	11	1	4	83	87	95
481–504	21	12	1	3	98	101	97
505–528	22	12	1	3	68	71	96
529–552	23	12	1	1	79	80	99
553–576	24	12	1	1	92	93	99

"dead" in the records for that sample (tables 11 and 12; fig. 27). The incidence of dead embryos in the samples increased rather consistently as development proceeded and was high in the later stages.

Overlapping was prominent between later stages since individual stages lasted from 4 to 16 days (table 6; fig. 28). Stage 13, the highest stage reached, had lasted 384 hours (16 days) when the experiment was finally terminated at 874 hours (ca. 37 days). Stages 12 and 13 overlapped 36 hours.

A most interesting feature of this experiment was the condition of embryos that finally reached and remained in stage 13. Although they were in stage 13, they were developing within the fertilization membrane (chorion). The spirally curled embryos developed transparent pericardia, pigment spots, and hemoglobin which had a muddy red to brown appearance in contrast to the normal bright pink to red. Some of these embryos finally were released when their membranes disintegrated. After release, however, the embryos did not straighten out or develop further but remained in this condition until death.

During this test several abnormalities were noted in the embryos: enlarged pericardia; straight tubular hearts; shorter but heavier bodies; enlarged gut region; a separation of yolk cells from the gut walls; and failure to straighten from the spirally curled position after removal of the chorion.

Development at 60° F.

The rate of development was much more rapid and the overlap of stages was less at 60° F. than at lower temperatures (tables 6, 13, and 14; fig. 28). The temperature of 60° F. was the lowest at which viable, burrowing prolarvae (stage 17) were produced. Mortality was generally less than on corresponding days in experiments at lower temperatures (fig. 27) and abnormalities were relatively few.

Table 11.—*Living and dead embryos per sample and their stage of development at 55° F. (12.8° C.)*

Sample	Hours	Number dead	Stage of living embryos												
			1	2	3	4	5	6	7	8	9	10	11	12	13
1	1	------	143	------	------	------	------	------	------	------	------				
2	3	------	80	8	------	------	------	------	------	------	------				
3	5	------	91	12	------	------	------	------	------	------	------				
4	7	------	27	53	------	------	------	------	------	------	------				
5	9	------	64	67	------	------	------	------	------	------	------				
6	11	------	32	114	------	------	------	------	------	------	------				
7	13	------	9	92	------	------	------	------	------	------	------				
8	15	22	------	91	19	------	------	------	------	------	------				
9	17	48	------	31	91	------	------	------	------	------	------				
10	19	14	------	56	65	------	------	------	------	------	------				
11	21	15	------	26	40	------	------	------	------	------	------				
12	23	47	------	5	34	48	------	------	------	------	------				
13	25	61	------	------	26	40	------	------	------	------	------				
14	27	83	------	------	16	35	------	------	------	------	------				
15	31	81	------	------	4	52	23	------	------	------	------				
16	35	81	------	------	------	9	75	------	------	------	------				
17	39	81	------	------	------	------	25	57	------	------	------				
18	43	62	------	------	------	------	11	16	------	------	------				
19	47	87	------	------	------	------	------	25	52	------	------				
20	51	70	------	------	------	------	------	------	36	39	------				
21	58	89	------	------	------	------	------	------	50	77	------				
22	71	118	------	------	------	------	------	------	50	75	------				
23	82	157	------	------	------	------	------	------	38	83	------				
24	95	151	------	------	------	------	------	------	40	81	------				
25	103	111	------	------	------	------	------	------	28	98	------				
26	116	133	------	------	------	------	------	------	------	135	------				
27	127	51	------	------	------	------	------	------	------	34	49				
28	139	89	------	------	------	------	------	------	------	82	59				
29	151	20	------	------	------	------	------	------	------	152	68				
30	163	226	------	------	------	------	------	------	------	------	61				
31	175	91									26	------	------	------	------
32	187	141									34	------	------	------	------
33	199	146									41	------	------	------	------
34	211	133									27	3	------	------	------
35	225	80									21	14	------	------	------
36	235	49									5	16	------	------	------
37	247	54									6	10	------	------	------
38	260	61									3	19	------	------	------
39	271	30									2	13	------	------	------
40	283	47									------	12	------	------	------
41	295	41									------	8	10	------	------
42	307	83									------	------	14	------	------
43	319	47									------	------	18	------	------
44	331	37									------	------	11	------	------
45	343	64									------	------	15	------	------
46	357	71									------	------	12	------	------
47	369	97									------	------	17	2	------
48	381	86									------	------	12	9	------
49	393	63									------	------	3	5	------
50	405	56									------	------	2	4	------
51	417	62									------	------	------	6	------
52	432	48									------	------	------	9	------
53	456	108									------	------	------	11	------
54	465	73									------	------	------	19	------
55	490	97									------	------	------	12	6
56	501	89									------	------	------	7	12
57	512	99									------	------	------	2	6
58	525	148									------	------	------	3	15
59	538	71									------	------	------	------	18
60	549	92									------	------	------	------	12

Table 12.—*Mortalities of sea lamprey eggs reared at a constant temperature of 55° F. (12.8° C.)*

[No sample on 24th day]

Time		Stage span	Number of samples	Number of embryos			Percentage dead
Hours	Days			Alive	Dead	Total	
0–24	1	0–4	12	1,298	146	1,444	10
25–48	2	4–7	7	466	536	1,002	54
49–72	3	7–8	3	327	268	595	45
73–96	4	7–8	2	242	308	550	56
97–120	5	7–8	2	261	244	505	48
121–144	6	8–9	2	224	140	364	38
145–168	7	8–9	2	291	246	537	46
169–192	8	9	2	60	232	292	79
193–216	9	9–10	2	71	279	350	80
217–240	10	9–10	2	56	129	185	70
241–264	11	9–10	2	38	115	153	75
265–288	12	9–10	2	27	77	104	74
289–312	13	10–11	2	32	124	156	79
313–336	14	11	2	29	84	113	74
337–360	15	11	2	27	135	162	83
361–384	16	11–12	2	40	183	223	82
385–408	17	11–12	2	14	119	133	89
409–432	18	12	2	15	110	125	88
433–456	19	12	1	11	108	119	91
457–480	20	12	1	19	73	92	79
481–504	21	12–13	2	37	186	223	83
505–528	22	12–13	2	26	247	273	90
529–552	23	13	2	30	163	193	84
577–600	25	13	1	15	113	128	88
601–624	26	13	1	18	93	111	84
625–648	27	13	1	12	125	137	91
649–672	28	13	1	5	104	109	95
673–696	29	13	1	12	126	138	91
697–720	30	13	1	9	86	95	91
721–744	31	13	1	10	108	118	92
745–768	32	13	1	6	61	67	91
769–792	33	13	1	4	109	113	96
793–816	34	13	1	6	103	109	94
817–840	35	13	1	8	108	116	93
841–864	36	13	1	8	128	136	94
865–888	37	13	1	3	105	108	97
875 [1]	37	------	1	------	16,250	16,250	100

[1] Terminal sample includes 11 live embryos mentioned in text as being incapable of survival.

Overlapping of stages was most limited with the exception of stages 1 and 2 (overlap of 3 samples) and the last 2 (stages 13 and 14) (overlap of 7 samples). Stage 13 was longest (127 hours or about 5 days). Stage 8 lasted more than 54 hours and was also represented in 8 samples (tables 6 and 13). Stage 14 was attained within 317 hours (about 13 days for first appearance).

Percentages of dead embryos in samples rose from a low of 32 percent during early cleavage stages (1–6) to 88 percent in the terminal sample. The rate of increase was highest in the early stages actually during the first 2 days. Percentage hatch (embryos that survived through stage 14) though not accurately measurable from the biased samples, obviously was good.

The relatively few abnormalities during this experiment (approximately 20 percent) took several forms, some of which were similar to those described earlier. Among the more common were enlargement of the pericardial area, and the straight tubular heart which, nevertheless, maintained a regular beat. Other specimens exhibited abnormal curvatures, balloon mouths, or cleft-lip. Abnormal curvatures of the trunk region produced embryos with "C," "J," "O," and "L" shapes. Balloon mouths were caused

TABLE 13.—*Living and dead embryos per sample and their stage of development at 60° F. (15.5° C.)*

Sample	Hours	Number dead	Stage of living embryos													
			1	2	3	4	5	6	7	8	9	10	11	12	13	14
1	1		143													
2	3		31	13												
3	4		14	20												
4	6	12	8	56												
5	8	11		38												
6	10	13		26												
7	13	17			26											
8	14	22			25											
9	16	29			9	14										
10	18	37				29										
11	20	24					17									
12	22	22					23	3								
13	24	53						23								
14	26	36						11								
15	28	31						4	13							
16	32	34							19							
17	36	30								12						
18	40	28								10						
19	44	28								23						
20	48	31								26						
21	54	17								15						
22	64	26								15						
23	76	16								13						
24	89	31								5						
25	100	20									15					
26	112	22									13					
27	124	26									14					
28	136	35									19	6				
29	148	23									5	7				
30	160	36										23				
31	172	29										11	7			
32	184	31											14			
33	196	55											5			
34	208	23											9	6		
35	220	37											2	12		
36	232	68												18		
37	244	40												20		
38	259	49												11		
39	283	45												9	16	
40	292	46													10	
41	317	51													20	4
42	328	36													4	5
43	339	35													8	12
44	352	5													1	6
45	365														5	3
46	376	3														
47	409	32													4	11

TABLE 14.—*Mortalities of sea lamprey eggs reared at a constant temperature of 60° F. (15.5° C.)*

[No sample on 17th day]

Time		Stage span	Number of samples	Number of embryos			Percentage dead
Hours	Days			Alive	Dead	Total	
0-24	1	0-6	13	518	240	758	32
25-48	2	6-8	7	118	218	336	65
49-72	3	8	2	30	43	73	59
73-96	4	8	2	18	47	65	72
97-120	5	9	2	28	42	70	60
121-144	6	9-10	2	39	61	100	61
145-168	7	9-10	2	35	59	94	63
169-192	8	10-11	2	32	60	92	65
193-216	9	11-12	2	20	78	98	80
217-240	10	11-12	2	32	105	137	77
241-264	11	12	2	31	89	120	74
265-288	12	12-13	1	25	45	70	64
289 312	13	13	1	10	46	56	82
313 336	14	13-14	2			120	
337-360	15	13-15	2			75	
361-384	16	13-15	2			31	
409-432	18	13-15	1			70	
433-456	19	15-16	1			22	
457-480	20	15-16	1			20	
481-504	21	16	1			16	
505-528	22	16	1			17	
529-552	23	16	1			42	
653-576	24	16	1			19	
577-600	25	17	1			18	
601-624	26	17	1			24	
625-648	27	17	1			35	
649-672	28	17	1			17	
673-696	29	17	1			12	
697-720	30	17	1			14	
721-744	31	17	1			8	
745-768	32	17	1			15	
769-792	33	17	1			7	
783 [1]	33	17	1	795	5, 606	6, 401	88

[1] Terminal sample.

from a failure of the stomadaeum to open. An enormous enlargement or ballooning of the pharyngeal region resulted, especially in the anterior portion, which tended to compress the branchial structures and cause them to become malformed and from all indication, non-functional.

A midline cleft in the dorsal lip was designated a "cleft-lip" abnormality.

Development at 65° F.

The rearing of sea lamprey eggs under constant temperature was more successful at 65° F. than at any lower or higher level (tables 15 and 16; fig. 27). Development was rapid (tables 6 and 15; fig. 28), overlapping of stages was practically nil, mortality was low, and abnormalities were few. The details offered in this section are based on an experiment conducted under refrigeration. Essentially the same results were obtained in experiments conducted with heat and the circulator.

Stages did not overlap at 65° F. with the exception of the overlap of stages 4 and 5 and of stages 13 and 14.

The percentage of dead embryos was low in most samples but the day-to-day variation of that percentage (fig. 27) was highly erratic and for several days the percentage exceeded that of the terminal sample taken on the 19th day. No verifiable explanation can be offered for this behavior of the percentages, but it is possible that dead eggs were not distributed evenly through the experimental lot and that certain samples happened to be taken from points at which dead embryos were concentrated. The 78-percent survival to the end of the experiment (only 22 percent dead in the terminal sample) was by far the highest

TABLE 15.—*Living and dead embryos per sample and their stage of development at 65° F. (18.4° C.)*

Sample	Hours	Number dead	Stage of living embryos													
			1	2	3	4	5	6	7	8	9	10	11	12	13	14
1	½	------	195	------	------	------	------	------	------	------						
2	1	------	330	------	------	------	------	------	------	------						
3	2	------	112	1	------	------	------	------	------	------						
4	3	------	------	279	------	------	------	------	------	------						
5	4	------	------	224	------	------	------	------	------	------						
6	5	------	------	433	------	------	------	------	------	------						
7	6	2	------	272	------	------	------	------	------	------						
8	7	1	------	287	------	------	------	------	------	------						
9	8	2	------	11	500	------	------	------	------	------						
10	9	3	------	------	169	------	------	------	------	------						
11	10	5	------	------	376	1	------	------	------	------						
12	11	3	------	------	51	307	------	------	------	------						
13	12	3	------	------	------	315	------	------	------	------						
14	13	12	------	------	------	303	62	------	------	------						
15	14	11	------	------	------	36	381	------	------	------						
16	15	9	------	------	------	4	274	------	------	------						
17	16	14	------	------	------	------	------	346	------	------						
18	17	14	------	------	------	------	------	329	------	------						
19	18	4	------	------	------	------	------	97	------	------						
20	19	14	------	------	------	------	------	19	324	------						
21	24	11	------	------	------	------	------	------	245	------						
22	28	24	------	------	------	------	------	------	------	476						
23	29	19	------	------	------	------	------	------	------	361						
24	30	23	------	------	------	------	------	------	------	329						
25	31	7	------	------	------	------	------	------	------	334						
26	32	10								208	------	------	------	------	------	------
27	45	9								218	------	------	------	------	------	------
28	53	22								227	------	------	------	------	------	------
29	56	81								247	------	------	------	------	------	------
30	64	91								7	189	------	------	------	------	------
31	69	82								------	304	------	------	------	------	------
32	80	65								------	337	------	------	------	------	------
33	93	65								------	365	------	------	------	------	------
34	104	231								------	96	78	------	------	------	------
35	116	181								------	------	161	------	------	------	------
36	128	113								------	------	99	194	------	------	------
37	142	284								------	------	------	61	------	------	------
38	152	80								------	------	------	74	258	------	------
39	164	6								------	------	------	------	139	------	------
40	176	118								------	------	------	------	231	------	------
41	188	179								------	------	------	------	135	------	------
42	200	51								------	------	------	------	64	171	------
43	212	107								------	------	------	------	------	170	------
44	224	100								------	------	------	------	------	60	------
45	236	97								------	------	------	------	------	84	------
46	248	38								------	------	------	------	------	39	43
47	271	3								------	------	------	------	------	20	135
48	285	5								------	------	------	------	------	10	129
49	296	6								------	------	------	------	------	19	205

TABLE 16.—*Mortalities of sea lamprey eggs reared at a constant temperature of 65° F. (18.4° C.)*

[No samples on 15th and 18th days]

Time		Stage span	Number of samples	Number of embryos			Percentage dead
Hours	Days			Alive	Dead	Total	
0–24	1	0–7	21	6, 283	108	6, 391	2
25–48	2	8	6	1, 926	92	2, 018	5
49–72	3	8–9	4	974	276	1, 250	22
73–96	4	9	2	702	130	832	16
97–120	5	9–10	2	335	412	747	55
121–144	6	10–11	2	354	397	751	53
145–168	7	11–12	2	471	86	557	15
169–192	8	12	2	366	297	663	45
193–216	9	12–13	2	405	158	563	28
217–240	10	13	2	144	197	341	58
241–264	11	13–14	1	--------	--------	120	--------
265–288	12	13–14	2	--------	--------	302	--------
289–312	13	13–15	2	--------	--------	384	--------
313–336	14	14–15	2	--------	--------	271	--------
361–384	16	15–16	1	--------	--------	31	--------
385–408	17	15–17	2	--------	--------	117	--------
433–456	19	17	1	--------	--------	114	--------
438 [1]	19	14–17	----------	11, 918	3, 355	15, 273	22

[1] Terminal sample.

among the experiments and represents unusually good results for the artificial rearing of fish eggs of any kind.

Abnormalities were extremely few, approximately 2 to 5 percent, mostly in the last samples. A few specimens had enlarged pericardia with a straight, tubular heart, and several had yolk separation and the associated hydrocoelus gut. One "twin" embryo was seen. These twins, in early stage 12, possessed a common but somewhat enlarged blastopore (fig. 29).

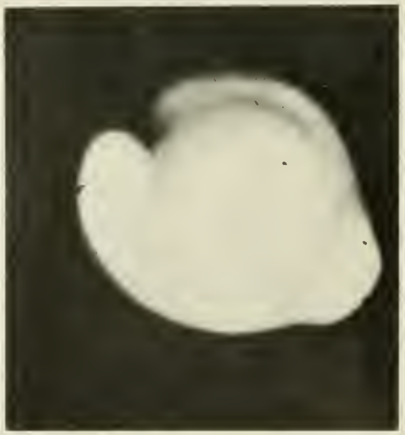

FIGURE 29.—Posterolateral view of twin embryos, showing the common, but enlarged, blastopore.

Development at 70° F.

The rate of development at 70° F. was only slightly accelerated over that at 65° F., in fact embryos reared at 70° F. reached stages 2 and 4 later than did those reared at 65° F. (table 6; fig. 28), and the limited overlap of stages characterized embryos at both temperatures. More pronounced and more significant were the increase of mortality (tables 17 and 18; fig. 27) and the greater number of abnormalities at 70° F. as compared with the "optimum" of 65° F.

At 70° F. as in the 65° test, the overlapping of stages was limited to a slight overlap between stages 11 and 12 and a somewhat greater one between stages 13 and 14 (tables 6 and 17). Elsewhere, the progression from one stage into the next was precise. Stage 8 was prolonged over 11 samples covering 32 hours, as against 2 to 3 for all other early stages.

Table 17.—*Living and dead embryos per sample and their stage of development at 70° F. (21.1° C.)*

Sample	Hours	Number dead	Stage of living embryos													
			1	2	3	4	5	6	7	8	9	10	11	12	13	14
1	1		277													
2	3		195													
3	5			130												
4	7	50		84	74											
5	9	8			121											
6	11	13			5	124										
7	13	43				56	93									
8	15	31					58	69								
9	17	39						45	96							
10	19	42							76	71						
11	21	41							39	81						
12	23	26								151						
13	25	40								113						
14	27	34								122						
15	31	38								138						
16	35	28								123						
17	39	38								135						
18	43	16								71						
19	47	45								99	24					
20	51	38								48	61					
21	58	65									122					
22	71	92									160					
23	82	89									62	31				
24	95	325										13				
25	103	221										58	61			
26	116	258											41	6		
27	127	44											12	53		
28	139	206												30		
29	151	139												5	35	
30	163	195													87	
31	175	64													33	13
32	187	48													15	20
33	199	25													18	26
34	211	46													8	44
35	225	24													1	32
36	235	24													1	41

Table 18.—*Mortalities of sea lamprey eggs reared at a constant temperature of 70° F. (21.1° C.)*

[No sample on 24tb day]

Time		Stage span	Number of samples	Number of embryos			Percentage dead
Hours	Days			Alive	Dead	Total	
0–24	1	0–8	12	1,845	293	2,138	14
25–48	2	8–9	7	825	239	1,064	22
49–72	3	8–9	3	391	195	586	33
73–96	4	9–10	2	106	414	520	80
97–120	5	10–12	2	166	479	645	74
121–144	6	11–12	2	95	250	345	72
145–168	7	12–13	2	127	334	461	72
169–192	8	13–14	2			193	
193–216	9	13–14	2			167	
217–240	10	13–15	2			160	
241–264	11	14–15	2			149	
265–288	12	15	2			124	
289–312	13	15–16	2			118	
313–336	14	16	2			32	
337–360	15	16–17	2			69	
361–384	16	17	2			91	
385–408	17	17	2			98	
409–432	18	17	2			21	
433–456	19	17	1			68	
457–480	20	17	1			109	
481–504	21	17	2			65	
505–528	22	17	2			59	
529–552	23	17	1			28	
577–600	25	17	1			29	
601–624	26	17	1			5	
625–648	27	17	1			50	
634 [1]	27	17	1	528	10,291	10,819	95

[1] Terminal sample.

The percentage of dead embryos in the samples rose rapidly to 80 percent on the fourth day and continued above 70 percent through the seventh day after which hatching made the further samples undependable as measured at mortality (table 18; fig. 27). The percentage of embryos dead in the 70°-terminal sample (95 percent) indicates final production a little less than half that at 60° F. (88 percent dead in 60° terminal sample).

Abnormalities in this experiment were relatively few (15 to 20 percent of the prolarvae), but more numerous than at 65° F. The abnormalities were similar to those listed for the 60° F. test, especially with respect to body shape.

Development at 75° F.

No viable, burrowing larvae were produced at a constant temperature of 75° F. Heavy mortality appeared early and persisted throughout development (tables 19 and 20; fig. 27) with the result that few embryos survived even to hatching. With the exception of stages 2 and 3 the various

Table 19.—*Living and dead embryos per sample and their stage of development at 75° F. (23.9° C.)*

Sample	Hours	Number dead	Stage of living embryos													
			1	2	3	4	5	6	7	8	9	10	11	12	13	14
1	1		129													
2	3	25	200													
3	5	25		113												
4	7	102			57	1										
5	9	186				40	2									
6	11	71				12	148									
7	13	81					113	40								
8	15	88						133	81							
9	17	85							177							
10	19	172								175						
11	21	191								102						
12	23	103								62						
13	25	53								89						
14	27	103								80						
15	31	163								89						
16	35	105								202						
17	39	54								69						
18	43	60								17	36					
19	47	207														
20	51	153									54					
21	58	268									81					
22	71	260									45	4				
23	82	322									8	23				
24	95	188										21	27			
25	103	287										4	26	3		
26	116	124											14	37		
27	127	202												13		
28	139	210												7		
29	151	265													14	
30	163	176													8	
31	175	106													1	11

Table 20.—*Mortalities of sea lamprey eggs reared at a constant temperature of 75° F. (23.9° C.)*

Time		Stage span	Number of samples	Number of embryos			Percentage dead
Hours	Days			Alive	Dead	Total	
0-24	1	0-8	12	1,585	1,129	2,714	42
25-48	2	8-9	7	582	745	1,327	56
49-72	3	9-10	3	184	681	865	79
73-96	4	9-11	2	79	510	589	87
97-120	5	10-12	2	84	411	495	83
121-144	6	12	2	20	412	432	95
145-168	7	13	2	22	441	463	95
169-192	8	13-14	2			325	
193-216	9	14-15	2			355	
217-240	10	15-16	2			265	
241-264	11	16	2			94	
265-288	12	16	1			27	
307 [1]	13		1		5,600	5,600	100

[1] Terminal sample.

stages were reached more rapidly than at lower temperatures and the overlap of stages was limited (tables 6 and 19; fig. 28).

Transition from one stage into the next was rather precise, as in the two preceding experiments. No stage overlapped another in more than 2 samples (tables 6 and 19). Stage 8 was projected over 9 samples covering 24 hours as contrasted with 2 or 3 for each of the earlier stages.

Substantial mortality appeared early at this temperature, especially between stages 0 and 8. The percentage of dead embryos had reached 95 percent on the seventh day, and the terminal sample did not include any live embryos. Production at this temperature was nil, despite the survival of some individuals as far as stage 16.

It is conceivable that stage 17 possibly could have been reached since the experiment was terminated when the supply of stage 16 prolarvae was exhausted. Were it possible to have allowed development to proceed without sampling, the probability of stage 17 being reached would have been improved.

Abnormalities occurred in 35 to 40 percent of the prolarvae. These abnormalities were similar to those already listed except that deformed specimens were especially numerous.

Development at 77.5° F.

A constant temperature of 77.5° F. was decidedly above the maximum at which sea lamprey eggs could develop successfully. Mortality was so great that all embryos were dead after 13 hours and none developed beyond stage 6, 32 cells (tables 6, 21, and 22; fig. 27).

Stage 1 was taken in the 1- to 4-hour samples, stage 2 in the 4- and 6-hour samples, and stage 3 in the 6- to 10-hour samples. Only 4 embryos developed beyond stage 3, and only 3 (stages 5 and 6) were still alive in the sample taken at 13 hours. All were dead in samples from 14 hours to the termination of the experiment at 24 hours. Some stages were reached earlier at 77.5° F. than at 75° F. (stages 2 and 3), but others were attained later at the higher temperatures (stages 4 and 5). See table 6 and fig. 28.

Table 21.—*Living and dead embryos per sample and their stage of development at 77.5° F. (25.3° C.)*

Sample	Hours	Number dead	Stage of living embryos					
			1	2	3	4	5	6
1	1		153					
2	3	1	67					
3	4	10	29	36				
4	6	58		32	4			
5	8	20			31			
6	10	64			8	1		
7	13	70					1	2

Table 22.—*Mortalities of sea lamprey eggs reared at a constant temperature of 77.5° F. (25.3° C.)*

Time		Stage span	Number of samples	Number of embryos			Percentage dead [1]
Hours	Days			Alive	Dead	Total	
0-24	1	0-6	13	364	708	1,072	66

[1] All embryos (485) dead in the 6 samples taken after 13 hours.

Development at 80° F.

Development was brief and erratic at a constant temperature of 80° F. A few embryos reached the 32-cell stage (stage 6) but most were dead long before that stage was reached (tables 6, 23, and 24; figs. 27 and 28).

No signs of cleavage had appeared at the end of the first 3 hours but at the fifth hour practically all of the eggs had begun to dimple, the initiation of first cleavage and stage 2. By the ninth hour all eggs had completed first cleavage and many had started the second cleavage (start of stage 3). At the 11th hour the pattern of cleavage had become rather erratic, since the second cleavage furrow often began while the first was less than half-completed. At times the first cleavage furrow seemed to regress.

Mortality which was slight in the first 2 samples had risen to about 35 percent in the seventh hour. All embryos were dead in the sample at 13 hours, but the next sample at 15 hours contained eggs that had reached stage 6 (32 cells) but had begun to vacuolate. All subsequent samples had only dead embryos.

Table 23.—*Living and dead embryos per sample and their stage of development at 80° F. (26.6° C.)*

Sample	Hours	Number dead	Stage of living embryos					
			1	2	3	4	5	6
1	3	6	131	------	------	------	------	------
2	5	7	107	16	------	------	------	------
3	7	85	35	131	------	------	------	------
4	9	124	------	11	55	------	------	------
5	11	149	------	------	31	------	------	------
6	13	165	------	------	------	------	------	------
7	15	303	------	------	------	------	------	2

Table 24.—*Mortalities of sea lamprey eggs reared at a constant temperature of 80° F. (26.6° C.)*

Time		Stage span	Number of samples	Number of embryos			Percentage dead [1]
Hours	Days			Alive	Dead	Total	
0–24	1	0–6	11	519	1,753	2,272	77

[1] Only 2 live embryos were taken after 11 hours and all (914) were dead after 15 hours.

SIGNIFICANCE OF OBSERVATIONS

Effect of temperature on development

The most significant result of the experimental rearing of sea lamprey eggs at 10 different constant temperatures (ranging from a minimum of 45° F. to a maximum of 80° F.) was the clear demonstration that successful development through to the production of viable burrowing larvae was possible only within a relatively narrow range. No live larvae were produced at any temperature below 60° F. or above 70° F. Further evidence of the extreme sensitivity of sea lamprey eggs to temperature comes from the much lower survival at 60° F. (12 percent), and 70° F. (5 percent), than occurs at the "optimum" temperature of 65° F. (78 percent). It is to be regretted that experiments were not made at 62.5° F. and 67.5° F. to define more clearly the trends within the 60°–70° range, but no further time was available when the importance of tests at these two intermediate temperatures became obvious.

Mortality was so heavy at the highest and lowest temperatures that all eggs had died before development had proceeded beyond very early stages. In general, the highest stage reached increased as the temperature approached the "successful" levels of 60°–70° F. This relationship is brought out by the following listing:

Temperature (F.)	*Highest stage reached*
45°	3 (4 cells)
50°	9 (gastrula)
52.5°	12 (head)
55°	13 (prehatching)
60°	17 (burrowing)
65°	17 (burrowing)
70°	17 (burrowing)
75°	16 (gill clefts)
77.5°	6 (32 cells)
80°	6 (32 cells)

Developmental abnormalities were least plentiful at 65° F. and increased as the temperature deviated from that value in either direction. In some tests the incidence was high, and the abnormalities (described briefly in the accounts of the experiments) involved monstrous distortions of the embryos.

In general, developmental rate (notably, the time required to reach the various stages) became faster, lengths of stages became shorter, and overlap between stages was lessened as temperature increased. Some of the exceptions to this statement no doubt represent the random variability of the data. Others, as for example, the seemingly depressing effect of the highest temperatures on the rate of development in the early stages may reflect a real cause-and-effect relationship.

The clear demonstration in the present studies that sea lamprey eggs are capable of full and normal development only within a relatively narrow temperature range brings out the great importance of controlling temperature at the correct level in developmental studies and experimental research. Consideration of the proper temperature had little place, nevertheless, in past studies of sea lamprey eggs. Authors failed to state the temperatures at which the eggs were reared or reared them at levels at which full, normal development could not be expected. Shipley (1885) did not state the temperature at which his sea lamprey embryos developed and McClure (1893) reared his embryos at 6°–7° C. (42.8°–44.6° F.). Damas (1948) mentioned temperatures of 12° and 18° C. (53.6° and 64.4° F.) on the development of *Lampetra* (it is not to be assumed, of course, that the effects of temperature on development are the same for *Petromyzon* and *Lampetra*, but certain parallels must be considered highly probable).

Shipley's account of the persistence of the blastopore and his statement that invagination took place at 130 hours suggest that embryos of the lamprey developed at a temperature of about 55° F. It appears then that neither he nor McClure conducted their experiments within the range at which normal development could be expected. If the relation of temperature to development in *Lampetra* is similar to that in *Petromyzon*, Damas' experiments at 18° C. (64.4° F.) should have been at nearly the optimum temperature, but those conducted 12° C. (53.6° F.) were well below the optimum. Thus, certain of the abnormalities (most of them duplicated in the present study, particularly at the higher and lower temperatures) that he interpreted as the effect of light intensity may actually have been caused by temperature.

Although the findings of the present experiments offer the strongest evidence that unsuitable temperatures may account for the failure of certain apparently suitable streams to produce larval sea lampreys, a too close application of the results to problems in nature is not advisable. The sea lamprey eggs were reared at constant temperatures in this study, whereas the temperatures in natural streams are subject to diurnal fluctuations, to substantial short-term increases and decreases along with changes of weather, and finally to a longer term, seasonal, upward trend as development proceeds. These fluctuations may have a profound effect on the tolerance of the developing egg. Temperature surely is an important, sometimes a critical, factor in the production of viable larvae in nature, but a good understanding of its operation would require controlled investigations in which eggs develop under fluctuating temperatures which are made to vary much as they do in natural streams.

LITERATURE CITED

Applegate, Vernon C.
1950. Natural history of the sea lamprey, *Petromyzon marinus*, in Michigan. U.S. Fish and Wildlife Service, Spec. Sci. Rept.: Fisheries, No. 55, 237 pp.

Applegate, Vernon C., and James W. Moffett.
1955. The sea lamprey. Sci. Amer., vol. 192, No. 4, pp. 36–41.

Applegate, Vernon C., and Bernard R. Smith.
1951. Sea lamprey spawning runs in the Great Lakes, 1950. U.S. Fish and Wildlife Service, Spec. Sci. Rept.: Fisheries, No. 61, 49 pp.

Applegate, Vernon C., Bernard R. Smith, and Alberton L. McLain.
1952. Sea lamprey spawning run in Great Lakes, 1951. U.S. Fish and Wildlife Service, Spec. Sci. Rept.: Fisheries: No. 68, 37 pp.

Augustinsson, K. B., R. Fange, A. Johnels, and E. Ostlund.
1956. Histological, physiological and biochemical studies on the heart of two cyclostomes, hagfish (*Myxine*) and lamprey (*Lampetra*). Jour. Physiol., vol. 131, pp. 257–276.

Creaser, Charles W.
1932. The lamprey *Petromyzon marinus* in Michigan. Copeia (3), p. 157.

Cresticelli, Frederick.
1956. The nature of the lamprey visual pigment. Jour. General Physiol., vol. 39, pp. 423–435.

Damas, H.
1944. Recherches sur le dèveloppment de *Lampetra fluviatilis*. Arch. de Biol., vol. 55, pp. 1–284.
1948. L'influence de la lumière sur la segmentation et la gastrulation chez *Lampetra fluviatilis*. Bull. Soc. Roy. Sci. Liège, Séance du 21 Oct., 1948, nos. 7–10, pp. 286–292.
1949. Nouvelles observations sur l'influence de la lumière sur le développment embryonaire de Lampetra. Jour. Cytoembryo. Belgo-neerland, Bd. 1949, pp. 96–99.

Daniel, J.
1931. Features in ammocoete development. Univ. California Publ , vol. 37, No. 4, pp. 41–52.

Gage, Simon H.
1928. The lampreys of New York State—life history and economics: Biological Survey of the Oswego River System, State of New York Conservation Department. Supplement to 17th Annual Report, 1927, pp. 158–191.

Gustafson, Trygve.
1950. Morphogenetic action of Li ion and chemical basis of its action. Rev. Suisse Zool., vol. 57, pp. 77–92.

Hatta, S.
1914. On the mesodermic origin and the fate of the so-called mesectoderm in *Petromyzon*. Proc. Roy. Soc. London, vol. 88, pp. 457–475.
1915. The fate of the peristomal mesoderm and the tail in *Petromyzon*. Annot. Zool. Japon., vol. 9, pp. 49–62.

Hubbs, Carl L.
1943. Terminology of early stages of fishes. Copeia 1943, No. 4, p. 260.

Hubbs, Carl L., and T. E. B. Pope.
1937. The spread of the sea lamprey through the Great Lakes. Trans. Amer. Fish. Soc., vol. 66 (1936), pp. 172–176.

Hubbs, Carl L., and Milton B. Trautman.
1937. A revision of the lamprey genus *Ichthyomyzon*. Misc. Publ., Univ. Michigan Mus. Zool., No. 35, 109 pp.

Jones, F. R. Hardin.
1955. Photokinesis in the ammocoete larva of the brook lamprey. Jour. Exp. Biol., vol. 32, pp. 492–503.

Lennon, Robert E.
1955. Artificial propagation of the sea lamprey, *P. marinus*, Copeia 1955, No. 3, pp. 235–236.

Loeb, Howard A.
1953. Sea lamprey spawning: Wisconsin and Minnesota streams of Lake Superior. U.S. Fish and Wildlife Service, Spec. Sci. Report: Fisheries No. 97, 36 pp.

Loeb, Howard A., and Albert E. Hall, Jr.
1952. Sea lamprey spawning: Michigan streams of Lake Superior. U.S. Fish and Wildlife Service, Spec. Sci. Rept.: Fisheries No. 70, 68 pp.

McClure, C. F. W.
1893. Notes on the early stages of segmentation in *P. marinus* L. Zool. Anzeiger, Bd. 16, S. 367–368; 373–376.

Mitchison, J. M.
1952. Optical changes in the membranes of the sea urchin egg at fertilization, mitosis and cleavage. Jour. Exp. Biol., vol. 29, pp. 357–362.

Sawyer, Wilbur H., and Willard D. Roth.
1954. The storage of biliverdin by the liver of the migrating sea lamprey, *P. marinus*. Anat. Rec., vol. 120, p. 93.

Selys-Longchamp, M. de.
1910. Gastrulation et formation des fuillets chez *Petromyzon planeri*. Arch. de Biol., vol. 25, pp. 1–75.

Shipley, A. E.
1885. On the formation of the mesoblast and the persistence of the blastopore in the lamprey. Proc. Roy. Soc. London, vol. 39, pp. 244–248.

Vladykov, Vadim D.
1949. Quebec lampreys. Department of Fisheries, Province of Quebec, Contribution No. 26, 67 pp.

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BLOOD PROPERTIES OF PRESPAWNING AND POSTSPAWNING ANADROMOUS ALEWIVES (*Alosa pseudoharengus*)

By CARL J. SINDERMANN AND DONALD F. MAIRS

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ABSTRACT

As part of a general investigation of the potential value of fish blood characteristics to the solution of population and migration problems, a study of modifications induced by environmental and physiological variables has been made. Six blood properties of prespawning and postspawning anadromous alewives (*Alosa pseudoharengus*) were compared. Changes that could be attributed to fresh-water migration and reproduction were found in only two of these properties; viz., significant reductions in average serum proteins and chlorides of postspawners. No important differences in average sedimentation rate, erythrocyte fragility, hemoglobin content, or serum electrophoretic pattern were found when fish entering fresh water in May were compared with seaward migrants 1 to 2 months later. Serum electrophoretic patterns were generally similar to those of other clupeoids, with fractions having mobilities comparable with human albumin and human alpha- and beta-globulins, but with little representation in the area of gamma-globulins. Great individual variations in hemoglobin content, total serum proteins, serum chloride, and sedimentation rate were found in alewives both before and after spawning.

BLOOD PROPERTIES OF PRESPAWNING AND POSTSPAWNING ANADROMOUS ALEWIVES (*ALOSA PSEUDOHARENGUS*)

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Dramatic changes in certain of the blood characteristics of humans and other higher vertebrates often occur under such physiological stresses as pregnancy or acute disease. It might be anticipated that lower vertebrates, with less precise control of their internal environment, would exhibit equally profound blood changes as the external medium or physiological conditions vary. As an adjunct to serological studies of fishes being carried on at the Bureau of Commercial Fisheries Biological Laboratory, Boothbay Harbor, Maine, it was considered important to assess the extent of environmental and physiological influences on blood properties, particularly those which might be related to serological reactions.

Erythrocyte antigens, which promise to be of great value in fish population and migration studies, have been examined most extensively in higher vertebrate groups (summarized by Dujarric de la Rivière and Eyquem, 1953; Mourant, 1954), where they have been found to be genetically determined and unmodified by environmental variations. Some evidence for genetic determination of fish erythrocyte antigens has been offered by Hildemann (1956). Serum components, which may also provide information of value to population studies, are in some cases subject to modification by other than genetic factors. For example, antibody production in fishes has been shown to vary with external temperature (Bisset, 1948) and protein fractions of fish serum to vary in amount in disease (Sindermann and Mairs, 1958). Because of possible influence of nongenetic factors on serological properties, a study of environmental and physiological effects on blood characteristics seemed advisable.

As part of such a study, this paper is concerned with the manner in which the combined stresses of migration from the sea to fresh water and of spawning are reflected in several blood characteristics of the alewife (*Alosa pseudoharengus*). The nature and extent of serum changes in prespawning and postspawning fish have received particular attention in this investigation, although observations on cellular blood components have been included.

MATERIALS AND METHODS

COLLECTION OF BLOOD SAMPLES

Prespawning and postspawning alewives were sampled in 1958 and 1959 from two separate Maine spawning runs—Damariscotta Mills and West Boothbay Harbor. Fish were first sampled in May, as they were about to enter fresh water, and again in late June and July, as they were about to re-enter the sea. In addition to the field samples, prespawning alewives taken from both runs were held without food in live cars and seawater tanks for 2 months before blood samples were taken, to determine the effect of starvation on electrophoretic characteristics of the serum.

The fish were bled by cardiac puncture, using a glass-needle technique developed in this laboratory (Perkins, 1957). Blood was collected in screw-top vials as individual samples. Half the samples were collected in vials containing 0.2 milliliter of 6-percent sodium citrate solution, and half were collected in vials without citrate. Determinations of hemoglobin content, sedimentation rate, and erythrocyte fragility were made immediately with the citrated samples. Sera from uncitrated blood samples were decanted after expressing from the clots overnight at 4° C. Individual serum samples were kept frozen at $-20°$ C. until determinations of chloride content, total

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serum protein content, and electrophoretic pattern were made. The sex and stage of gonad development of each fish were recorded when the blood sample was taken.

DETERMINATIONS OF BLOOD PROPERTIES

Hemoglobin Content

Determination of the hemoglobin content of individual citrated blood samples was made with the cyanmethemoglobin method, using reagent and standard supplied by Hycel Hormone Chemistry Laboratory, Houston, Tex. With a Sahli pipette, .02 ml. blood was added to 5 ml. cyanmethemoglobin reagent and thoroughly mixed. Contents were transferred after 15 minutes to a cuvette and read colorimetrically with a Photovolt Lumetron colorimeter at a wavelength of 530 millimicrons. The colorimeter reading was transferred to a standard hemoglobin curve and hemoglobin concentration obtained in grams per 100 ml.

Sedimentation Rate

The rate of settling of erythrocytes was determined with a standard Westergren blood sedimentation apparatus. Individual samples of citrated blood was drawn into Westergren pipettes to the 100-millimeter mark and placed vertically in a Westergren rack. The number of millimeters that the erythrocytes had dropped at the end of 1, 2, and 3 hours—the actual sedimentation—was recorded and multiplied by 2 to make results comparable with standard tests that use the entire 200-mm. pipette length. Results are expressed in terms of the standard 200-mm. length.

Erythrocyte Fragility

Sodium chloride solutions ranging from 0.3 to 1.5 percent in 0.1-percent increasing steps were used to test erythrocyte fragility. For each sample, .05 ml. of a 50-percent cell suspension was added to 1 ml. of each saline dilution and readings of "no hemolysis," "partial hemolysis," or "complete hemolysis" were recorded for each tube at the end of 1 hour's incubation at 4° C.

Total Serum Proteins

The biuret method of Kingsley (1942) was used to determine total serum proteins. This involves precipitation with acetone-alcohol followed by addition of biuret reagent. Readings were made with a Photovolt Lumetron colorimeter at a wave length of 530 millimicrons and were plotted against a standard curve prepared with dilutions of clinical chemistry control serum, supplied by Hyland Laboratories, Los Angeles, Calif., to obtain total protein values.

Serum Chlorides

Determinations of serum chlorides were made by the standard method outlined in the manual for Photovolt Lumetron colorimeter. This involves treatment of serum with tungstic acid, silver iodate, phosphoric acid, and potassium iodide. Readings were made with the Lumetron colorimeter at a wave length of 420 millimicrons and plotted against a standard curve prepared from known chloride concentrations to obtain serum chloride values.

Serum Electrophoresis

Electrophoretic examination of serum was made with a Spinco paper electrophoresis system. Samples were run for 6 hours at 15 milliamperes, with veronal buffer of pH 8.6 and ionic strength of .05. Pooled human serum was used as a standard with each series. Filter-paper strips were dyed with bromphenol blue and analysed with a Spinco Analytrol densitometer.

COMPARISON OF BLOOD PROPERTIES

Tests of serum and cellular components of the blood of prespawning and postspawning alewives provided the data presented in table 1. Results from the two Maine spawning runs have been combined, since no consistent differences between them were noted.

HEMOGLOBIN

Variations in hemoglobin content of fish blood have been examined in a number of marine and fresh-water species by several investigators. Black (1955) found that the hemoglobin level of largemouth bass increased after forced exercise, but that of five other fish species did not. Pavlov and Krolik (1936) found that hemoglobin increased with the ripening of the sex products, while Naumov (1956) noted that it increased to the time of spawning and then dropped to a very low level. Gelineo (1957) found that hemoglobin values for several species of marine fish were some-

TABLE 1.—*Comparison of six blood properties of prespawning and postspawning alewives*

[Range in parentheses]

Blood property	Method of determination	Prespawning		Postspawning	
		Number of fish tested	Average	Number of fish tested	Average
Hemoglobin	Cyanmethemoglobin, Lumetron colorimeter	79	9.5 g./100 ml. (4.5–12.5)	50	9.4 g./100 ml. (4.0–13.0)
Sedimentation rate	Westergren apparatus	70	4.9 mm. (2.0–9.6)	51	4.7 mm. (1.0–12.0)
Erythrocyte fragility	Saline dilutions: 0.3 to 1.5 percent	60	0.6 percent (0.5–0.7)	60	0.6 percent. (0.5–0.7)
Total serum proteins	Biuret method of Kingsley (1942), Lumetron colorimeter.	40	5.9 g./100 ml. (3.9–8.6)	43	5.3 g./100 ml. (2.7–6.9)
Serum chloride	Lumetron colorimeter	30	430 mg./100 ml. (355–458)	28	395 mg./100 ml. (302–440)
Serum electrophoresis	Spinco model-R paper electrophoresis system	121	(1)	65	(1)

[1] See fig. 4.

what higher during the period of sexual activity than at other times. Findings in the present study indicated that average hemoglobin content of alewives entering fresh water to spawn is not different from that of the spent fish returning to the sea after spawning. Prespawners had an average hemoglobin value of 9.5 g. per 100 ml. (range, 4.5–12.5), while postspawners had an average of 9.4 g. per 100 ml. (range 4.0–13.0).

SEDIMENTATION RATES

The settling rate of erythrocytes has wide clinical use as an indicator of certain physiological changes. It is higher in human females than males and is greater during pregnancy and in disease. In fishes, Schumacher, Hamilton, and Longtin (1956) found that furunculosis caused a marked increase in the sedimentation rates of brook trout, while Kalashnikov (1939) found that the sedimentation rate increased as the gonads matured.

The present study indicated great individual differences in sedimentation rates of both prespawning and postspawning alewives (range, 1.0 to 12.0 mm. at 3 hours for 121 fish). However, no important changes have been disclosed by comparison of average sedimentation rates of fish entering fresh water to spawn with those of spent members of the same populations leaving fresh water 2 months later. Average sedimentation rates for prespawners were 1.2 mm. at 1 hour, 3.3 mm. at 2 hours and 4.9 mm. at 3 hours; for postspawners, 1.1 mm. at 1 hour, 3.2 mm. at 2 hours, and 4.7 mm. at 3 hours (fig. 1). Ripe females exhibited higher average sedimentation rates than did ripe males (5.4 mm. compared with 4.3 mm. in 3-hour readings), but this difference disappeared in postspawners.

ERYTHROCYTE FRAGILITY

Another indication of physiological distress is the lowered ability of red blood cells to withstand decreasing osmotic pressure of the surrounding medium. Fragility of human erythrocytes increases in certain diseases. Examination of alewife blood disclosed no changes in cell fragility due to the spawning migration. One-hour tests showed that complete lysis occurred consistently at between 0.5- and 0.7-percent saline in both prespawning and postspawning fish.

TOTAL SERUM PROTEINS

The serum proteins of animals have a variety of chemical and physical functions, including their important role in osmotic regulation. Among the invertebrates, wide individual variations (2.2 g. to 10.2 g. per 100 ml.) in total serum proteins of the lobster (*Homarus americanus*) and even greater variations (1.16 g. to 13.75 g. per 100 ml.) in the crab (*Cancer magister*) were noted by Leone (1953). In fishes, average total proteins of 5.6 g. per 100 ml. for adult salmon (*Salmo salar*), and 4.9 g. per 100 ml. for *Conger vulgaris* were reported by Drilhon, Fine, and Daoulas (1958). Keys (1933) found that the total serum proteins of eels dropped from 8.4 g. per 100 ml. in sea water to 6.8 g. per 100 ml. in fresh water.

The present study of prespawning and postspawning alewives has disclosed marked individual variations in total serum proteins—from 3.9 to 8.6 g. per 100 ml. in prespawners, and from 2.7 to 6.9 g. per 100 ml. in postspawners (fig. 2)

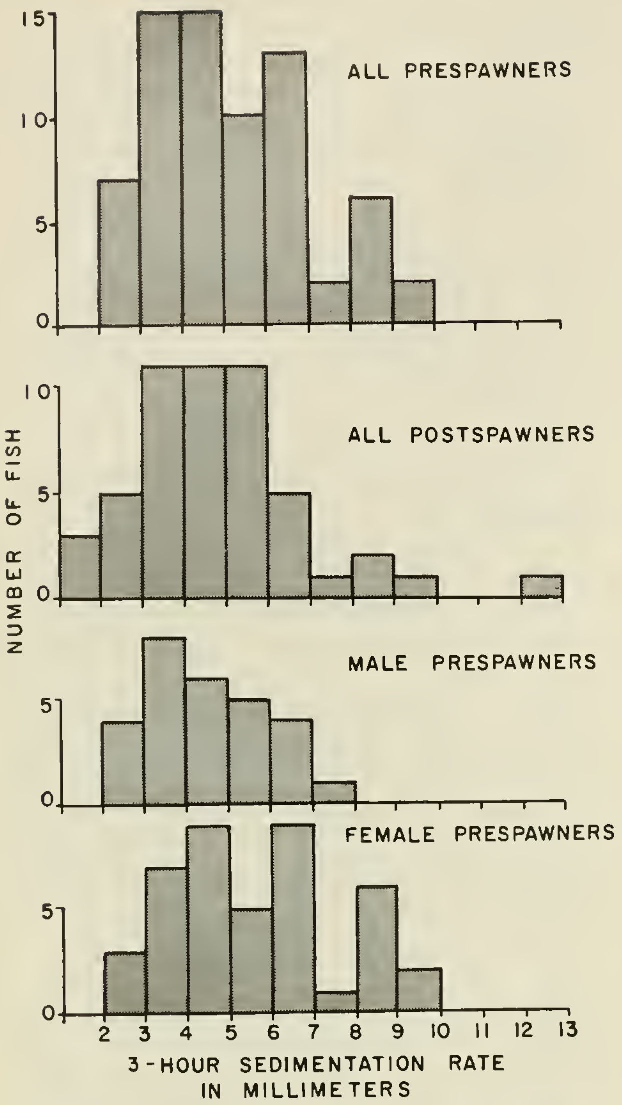

Figure 1.—Three-hour sedimentation rates for prespawning and postspawning alewives.

The average for prespawners was 5.9 g. per 100 ml. while that for postspawners was 5.3 g. per 100 ml.—a reduction in fresh water significant at the 5-percent level with the student T-test used for small samples, as well as with the rank sum test.

SERUM CHLORIDES

Concentrations of various ions in animal body fluids, particularly in invertebrates, may vary with environmental and physiological conditions (Prosser, 1950). The closed circulatory system of vertebrates probably effects greater ionic stability than is true for invertebrates. Numerous studies of teleost ionic regulation in varying external salinities have been made (reviewed by Fontaine and Koch, 1950, and Black, 1957). Keys (1933) found that serum chlorides of eels (*Anguilla anguilla*) were lower in fresh water than in the sea (480 milligrams per 100 ml. as opposed to 580 mg. per 100 ml.). Bond, Cary, and Hutchinson (1932) and McFarland and Munz (1958) found that in hagfish (*Polistotrema stouti*) the concentration of blood chloride varied in a linear manner with that of the surrounding medium. Harris (1959) noted a drop in blood chloride from 804 mg. to 683 mg. per 100 ml. when *Fundulus heteroclitus* were transferred from salt water to fresh.

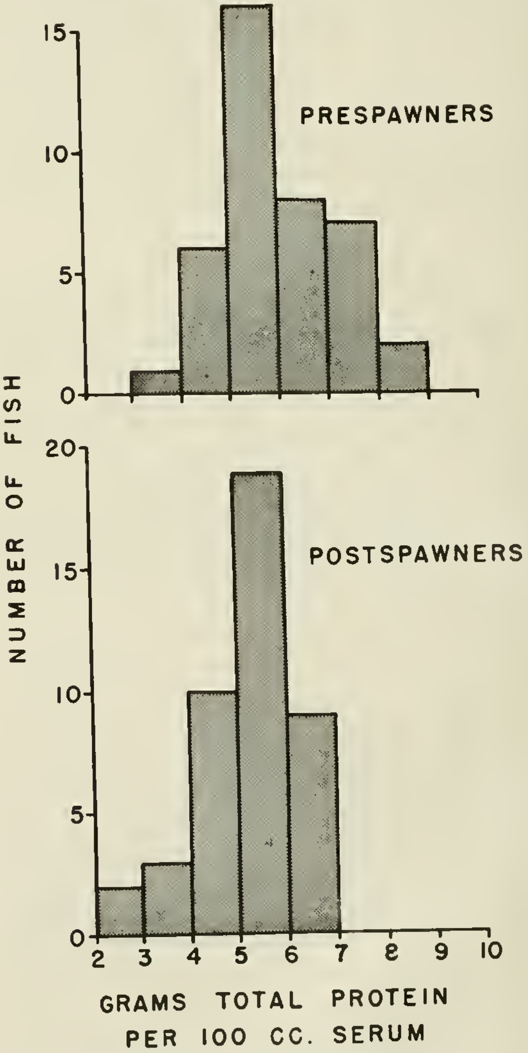

Figure 2.—Variation in total serum proteins in alewives before and after spawning.

The present study of serum chlorides in alewives has provided an average value of 430 mg. per 100 ml. for fish from the sea, taken just before the fresh-water migration. A decrease to an average of 395 mg. per 100 ml. was found for fish taken in fresh water just before their seaward migration (fig. 3). Within the limitations of a small sample size (30 prespawners, 28 postspawners), the rank sum test showed this decrease to be significant. As with serum proteins, individual variations in serum chlorides were marked (355 mg. to 458 mg. per 100 ml. in prespawners; 302 mg. to 440 mg. per 100 ml. in postspawners).

Comparison of these data with those of Keys (1933), which were drawn from nonspawning samples, suggests that the observed chloride reductions in alewife sera were probably associated with lower environmental salinity rather than with spawning activities. The average serum chloride of alewives in fresh water is quite similar to that of carp (401 mg. per 100 ml.) reported by Field, Elvehjem, and Juday (1943), but is somewhat lower than that of brown trout (424 mg. per 100 ml.) reported by Phillips and Brockway (1958).

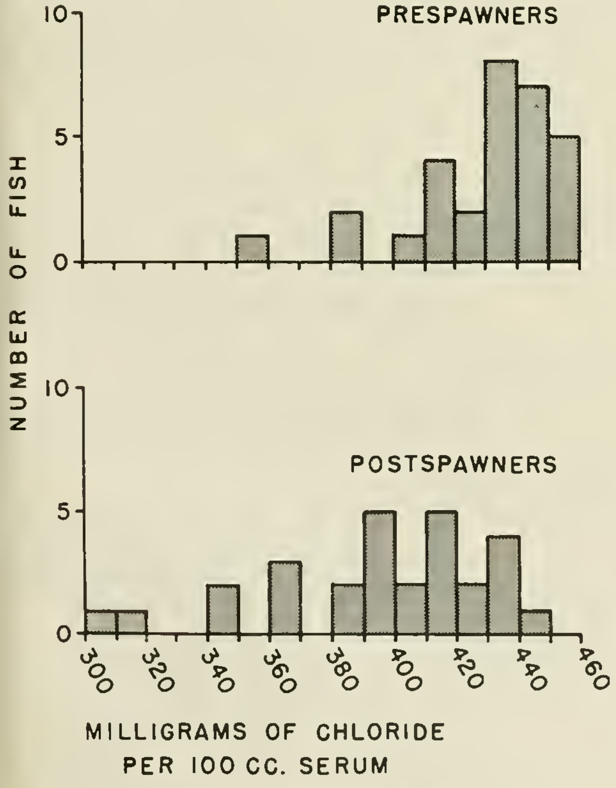

FIGURE 3.—Serum chlorides of prespawning and postspawning alewives.

SERUM ELECTROPHORETIC PATTERNS

Electrophoretic studies of fish sera have disclosed patterns which appear to be species specific (Deutsch and Goodloe, 1945; Moore, 1945). However, Drilhon et al. (1956) noted quantitative changes in albumin and beta-globulins when starved trout were compared with well-fed fish. Sindermann and Mairs (1958) found that acute fungus disease caused a drastic reduction in the albumin fraction of sea-herring blood serum. Drilhon, Fine, and Daoulas (1958) reported that neither fresh-water migration nor stage of maturity had an effect on electrophoretic patterns in trout and salmon.

The present study of prespawning and postspawning alewives has disclosed no major changes in serum patterns attributable to reproduction or to fresh-water migration. Serum patterns of alewives resembled those of other clupeoids and teleosts in general (Woods and Engle, 1957; Sindermann and Mairs, 1958) in that fractions with mobilities similar to human albumin, alpha-globulins, and beta-globulins, were consistently present. A characteristic electrophoretic serum pattern for alewives is graphed in figure 4. Fraction I, represented by the lead anodal peak, had a mobility slightly less than human albumin; fraction II occurred as a peak with mobility similar to human alpha-2 globulin; and fraction III migrated variably in the vicinity of human beta-globulin, in

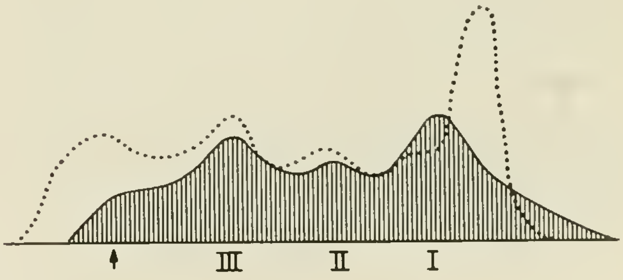

FIGURE 4—Electrophoretic pattern of alewife serum (shaded curve) compared with pattern of normal human serum. Samples were applied at a point indicated by the arrow, and the anode is to the right.

some cases occurring in two separate peaks. Little representation was found in the zone of human gamma-globulin. Fraction I slumped drastically in serum from alewives held experimentally in sea water under starvation conditions for 2 months; and is in general agreement with Keys' (1933) finding of lower total serum protein values for starved eels.

SUMMARY AND CONCLUSIONS

Comparison of six blood properties of prespawning and postspawning alewives (*Alosa pseudoharengus*) from two runs disclosed modifications in only two characteristics that could be attributed to fresh-water migration or spawning. Total serum proteins of postspawners averaged 5.3 g. per 100 ml., while prespawners averaged 5.9 g. Similarly, serum chlorides were reduced in postspawners to 395 mg. per 100 ml. from a previous average of 430 mg. Hemoglobin values, erythrocyte fragility, sedimentation rates, and electrophoretic patterns were unchanged. Hemoglobin values for alewives averaged 9.5 g. per 100 ml., with a range of 4.0 to 13.0. Complete lysis of alewife erythrocytes occurred, with little variation, between 0.5- and 0.7-percent saline in 1-hour tests. Sedimentation rates averaged 1.2 mm. for 1 hour, 3.3 mm. for 2 hours, and 4.8 mm. for 3 hours. In electrophoretic studies of serum proteins, fractions with mobilities similar to human albumin and human alpha- and beta-globulins, were found. Of these, only the beta fraction was variable, and no consistent changes resulting from fresh-water migration or spawning were observed.

The data indicated little change in most of the blood properties studied, when prespawning and postspawning alewives were compared—suggesting relative stability of the characters during this time of physiological stress. It should be noted, however, that a period of at least 1 month separated the tests of the two groups, and that no examinations were made of fish actually spawning. Recovery from any short-term effects of reproduction could have been accomplished before alewives were sampled again as seaward migrants.

Marked individual variations in such properties as sedimentation rate, hemoglobin values, serum chloride concentration, and total serum protein concentration are consistent with findings for other lower vertebrate species (Hunn, 1959, presents a list of pertinent references.) No clear association of individual variations with gonad condition, sex, or environmental salinity has been made, although the average sedimentation rate for ripe females was somewhat higher than that for ripe males. Average total serum proteins and chlorides were significantly higher in prespawners caught in salt water than in postspawners taken in fresh water—probably a reflection of environmental salinity.

Further studies are planned to assess the influences of environmental and physiological factors on the blood characteristics of fishes. In many ways, the alewife is the animal of choice for this work. Serological studies may be made with the same blood samples that are tested for other blood properties. Furthermore, offspring of small, isolated alewife populations may be examined before their seaward migration and compared with spawning adults. Also, spawning runs widely separated geographically—from the Middle Atlantic States to the Gulf of Saint Lawrence—may be compared. Finally, since landlocked populations of this species occur in North America, they may be compared with anadromous stocks.

LITERATURE CITED

Bisset, K. A.

1948. The effect of temperature upon antibody production in cold-blooded vertebrates. Journal of Pathology and Bacteriology, vol. 60, no. 1, p. 87–92.

Black, Edgar C.

1955. Blood levels of hemoglobin and lactic acid in some fresh-water fishes following exercise. Journal of the Fisheries Research Board of Canada, vol. 12, no. 6, p. 917–929.

Black, Virginia S.

1957. Excretion and osmoregulation. *In* The Physiology of Fishes (Margaret E. Brown, ed.), vol. I, p. 163–205. Academic Press, New York, 447 p.

Bond, Richard M., M. Katharine Cary, and G. E. Hutchinson.

1932. A note on the blood of the hagfish, *Polistotrema stouti* (Lockington). Journal of Experimental Biology, vol. 9, no. 1, p. 12–14.

Deutsch, H. F., and M. B. Goodloe.

1945. An electrophoretic survey of various animal plasmas. Journal of Biological Chemistry, vol. 161, no. 1, p. 1–20.

Drilhon, Andrée M., J. M. Fine, and Francoise Daoulas.
1958. Étude électrophorétique de quelques constituants sériques des poissons. Annales de l'Institut Oceanographique (Monaco), vol. 35, no. 2, p. 141–158.

Drilhon, Andrée, Jean Fine, José Uriel, and Francoise Lebourdelles.
1956. Étude électrophorétique des constituants du sérum de l'Anguille. Comptes-Rendus des Séances de l'Académie des Sciences (Paris), vol. 243, no. 22, p. 1802–1805.

Dujarric de la Rivière, R., and A. Eyquem.
1953. Les groupes sanguins chez les animaux. Éditions Médicales Flammarion, Paris, 416 p.

Field, John B., C. A. Elvehjem, and Chancey Juday.
1943. A study of the blood constituents of carp and trout. Journal of Biological Chemistry, vol. 148, no. 2, p. 261–269.

Fontaine, M., and H. Koch.
1950. Les variations d'euryhalinité et d'osmorégulation chez les poissons. Journal de Physiologie (Paris), vol. 42, no. 2, p. 287–318.

Gelineo, Stefan.
1957. Le taux de l'hémoglobine sanguine de plusieurs espèces de poissons de mer. Comptes-Rendus des Séances de la Sociéte de Biologie (Paris), vol. 151, nos. 8–9, p. 1594–1597.

Harris, Patricia J.
1959. A study of thyroid function in *Fundulus heteroclitus*. Biological Bulletin, vol. 117, no. 1, p. 89–99.

Hildemann, W. H.
1956. Goldfish erythrocyte antigens and serology. Science, vol. 124, no. 3216, p. 315–316.

Hunn, Joseph B.
1959. The chemistry of fish blood, a bibliography. U.S. Army Chemical Warfare Laboratories, Special Publication 2–22, p. 1–22.

Kalashnikov, G. N.
1939. [The speed of sedimentation of the erythrocytes of fishes. Research Notes Moscow State University, ed. 33.] (In Russian; original paper not seen by authors.)

Keys, Ancel.
1933. A mechanism of adaptation to varying salinity in the common eel and the general problem of osmotic regulation in fishes. Proceedings of the Royal Society of London, vol. B112, no. 776, p. 184–199.

Kingsley, George R.
1942. The direct biuret method for the determination of serum proteins as applied to photoelectric and visual colorimetry. Journal of Laboratory and Clinical Medicine, vol. 27, p. 840–845.

Leone, Charles A.
1953. Preliminary observations on intraspecific variation of the levels of total protein in the sera of some decapod crustacea. Science, vol. 118, no. 3063, p. 295–296.

McFarland, William N., and Frederick W. Munz.
1958. A reexamination of the osmotic properties of the Pacific hagfish, *Polistotrema stouti*. Biological Bulletin, vol. 114, no. 3, p. 348–356.

Moore, Dan H.
1945. Species differences in serum protein patterns. Journal of Biological Chemistry, vol. 161, no. 1, p. 21–32.

Mourant, A. E.
1954. The distribution of the human blood groups. Blackwell Scientific Publications, Oxford. 438 p.

Naumov, V. M.
1956. [Ovogenesis and ecology of the sexual cycle of the Murmansk herring (*Clupea harengus harengus* L.).] Transactions of Knipovich Polar Science Institute of Sea Fisheries and Oceanography (Murmansk), vol. 9, p. 176–225. (In Russian.)

Pavlov, V. A., and B. E. Krolick.
1936. [The hemoglobin content and number of erythrocytes in the blood of some fresh-water fishes.] Transactions of the Borodino Biological Station, vol. 9, no. 1. (In Russian; original paper not seen by authors.)

Perkins, Frank E.
1957. A field technique for obtaining samples of fish blood serum. Progressive Fish-Culturist, vol. 19, no. 3, p. 144.

Phillips, Arthur M., jr., and Donald R. Brockway.
1958. The inorganic composition of brown trout blood. Progressive Fish-Culturist, vol. 20, no. 2, p. 58–61.

Prosser, C. L. (Ed.)
1950. Comparative animal physiology. W. B. Saunders Co., Philadelphia. 888 p.

Schumacher, R. E., C. H. Hamilton, and E. J. Lonotin.
1956. Blood sedimentation rates of brook trout as affected by furunculosis. Progressive Fish-Culturist, vol. 18, no. 4, p. 147–148.

Sindermann, Carl J., and Donald F. Mairs.
1958. Serum protein changes in diseased sea herring. Anatomical Record, vol. 131, no. 3, p. 599–600.

Woods, Kenneth R., and Ralph L. Engle.
1957. Phylogenesis of plasma proteins and plasma cells. I. Starch gel zone electrophoresis of sera from marine invertebrates and fishes. (Abstract.) Biological Bulletin, vol. 113, no. 2, p. 362–363.

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EFFECTS OF COPPER ORE ON THE ECOLOGY OF A LAGOON

By KENNETH T. MARVIN, LARENCE M. LANSFORD, and
RAY S. WHEELER

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ABSTRACT

A large-scale experiment was conducted in a lagoon, off the Galveston Ship Channel in the Gulf of Mexico, to determine the feasibility of using copper ore as a control for destructive plankton blooms. A chemical and biological study was made of the lagoon for a period of 9 months previous to the addition of 60 tons of copper ore. Comparison with a similar study made after the addition of the ore revealed that the ore did not have the desired qualities of control; therefore its use for control was not recommended.

EFFECTS OF COPPER ORE ON THE ECOLOGY OF A LAGOON

By Kenneth T. Marvin and Larence M. Lansford, *Chemists*, and Ray S. Wheeler, *Fishery Research Biologist*, Bureau of Commercial Fisheries

Sudden, immense increase in the plankton population has resulted in extensive destruction of commercially important fish and shellfish. Sometimes this fish-killing plague is known as "red tide" because of the amber to dull-red discoloration of the water.

The organism present in frequent occurrences of red tide in Offats Bayou, Galveston (Tex.) was identified by Gunter (1942), and by Gates and Wilson (1960), as *Gonyaulax monilata*. *Gymnodinium breve* was identified by Davis (1948) as the cause of destructive red tide blooms that have occurred off the west coast of Florida at irregular intervals since, at least, 1844 (Feinstein and others, 1955).

Following the outbreak of destructive *G. breve* blooms in 1946 and 1947, the U.S. Bureau of Commercial Fisheries began a study of the organism and the environmental factors limiting or promoting its growth, to develop, if possible, a means of controlling or, at least, reducing the occurrence of these lethal outbreaks.

The toxic property of copper has been employed elsewhere with varying degrees of success in related occurrences of plankton blooms. Experiments in the U.S. Fish and Wildlife Service Laboratory have demonstrated that the minimum amount of dissolved copper lethal to *G. breve* is about 0.5 microgram atoms per liter (0.03 p.p.m.). An experiment was designed therefore to test the feasibility of using immersed copper ore as a source of copper in lethal concentrations through its release into solutions over a rather long period of time.

We wish to express our appreciation to Mrs. Zoula Zein-Eldin, William Wilson, and Drs. David Aldrich and Abraham Fleminger, who conducted many of the analyses, and to the Morenco Mining Branch of the Phelps Dodge Copper Corporation for furnishing the copper ore for the experiment.

COPPER ORE EXPERIMENT

The experiment was designed to determine whether or not immersed ore would affect the flora and fauna. This would be decided by comparing chemical and biological studies made before and after the addition of ore.

Questions to be resolved were the following:

(1) Could copper concentration in a body of water be raised to a level lethal to *G. breve* by the permanent exposure of a reasonable amount of copper ore? (2) Would the copper concentration of the water remain at a constant level? (3) Would the copper have an adverse effect on other marine organisms?

To obtain an estimate of the amount of copper ore needed, laboratory studies were made on the solubility of the copper in various amounts of ore in tanks of sea water. On the basis of the results of these tests, 20 tons of ore seemed a reasonable amount with which to start. Subsequent dosages, if necessary, would be based on the results of the first addition. We used a sulphide ore that contained approximately 1 percent copper and 3.5 percent iron. The particle size varied from dust to coarse gravel.

The questions were answered (1) by observing the effects of the ore on two indicator organisms,[1] (2) by determining the level of the copper concentration maintained, and (3) by comparing ecological conditions of the lagoon before and after the addition of the ore. Comparisons were based on gross differences in productivity of the water, on significant changes in mortality rates of organisms, and on variation in barnacle setting rate. Chlorophyll and zooplankton analyses were used as indicators of productivity. Mortality rate

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[1] Laboratory experiments demonstrated that the tolerance of these organisms to copper was approximately the same as that of *Gymnodinium breve* One of these, *Prorocentrum* sp., was placed in the lagoon in dialysis bags, another, *Gymnodinium splendens*, occurred naturally in the lagoon.

NOTE.—Approved for publication September 12, 1960. Fishery Bulletin 184

studies were made of *Gymnodinium splendens* that occurred in the water, and of organisms from the live car: oysters, *Crassostrea virginica*; mullet, *Mugil cephalus*; and two snails, *Littorina irrorata* and *Thais* species.

Our field activities were conducted in a man-made lagoon located on the eastern end of Galveston Island (fig. 1). The lagoon, 1.1 statute miles long, has an estimated volume of about 230 acre-feet and is connected to the Galveston Ship Channel by seven 36-inch cement culverts. Chemical and biological samples were taken at eight stations. Samples were collected three to four times a week until the first ore addition of 20 tons was made and then twice a week. Several months after the final addition of 40 tons, the rate was reduced to once a week and the number of stations sampled to three (stations 1, 4, and 7). During collection trips samples were taken for salinity, copper, chlorophyll, *G. splendens*, and zooplankton analyses. The water for these was taken with a stainless steel neoprene impeller pump. During collections the intake end of the polyethylene connection hose was continuously raised and lowered from a few inches of the bottom to the surface. Thus, the samples were representative of the entire column. A 4-inch Secchi disc reading was also taken at each station. Once or twice a week, depending on weather conditions, a count was made of the organisms in the live cars anchored at each station. At weekly intervals, barnacle-setting plates were suspended 2 feet below the surface at each station. These plates were replaced every week.

Before each addition of ore, dialysis bags containing cultures of known concentrations of *Prorocentrum* sp. were suspended in perforated polyethylene bottles 2 feet below the surface at stations 2, 4, 5, 6, and 7. These bottles were replaced so that some of them remained in the water for 2 days and others for 4 days. The first of these experiments was discontinued 2 weeks after the first ore addition and the second, 1 week after the second addition.

ANALYTICAL METHODS

Chlorophyll

The chlorophyll analyses consisted of estimations of chlorophyll a, b, and c in acetone extracts of plant and animal material. The method employed was that of Richards with Thompson (1952) as modified by Creitz and Richards (1955).

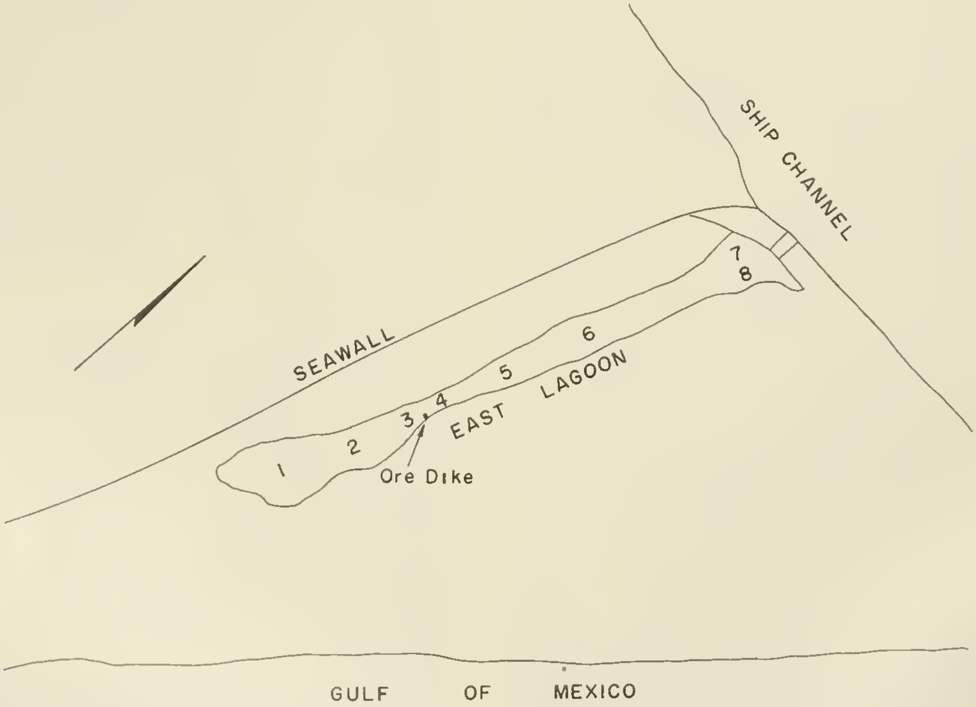

FIGURE 1.—East Lagoon station locations selected for the copper ore experiment.

Salinity

Salinity values were estimated from density-temperature measurements taken with a hydrometer calibrated to the nearest 0.2 of a salinity unit (⁰/₀₀) and a centigrade thermometer calibrated to the nearest unit.

Gymnodinium splendens

Two-liter water samples for *G. splendens* analyses were placed under fluorescent lights for about 16 hours. This concentrated the organisms in the upper part of the container. A preliminary examination was made of a portion of the sample taken from the meniscus. If *G. splendens* were not observed, a zero count was assumed for the sample. If in evidence, the top 200 ml., which contained virtually all of the *G. splendens*, were carefully siphoned into a flask and thoroughly mixed. Ten 1-milliliter samples were removed and counted for *G. splendens*. The average of these was converted to count per liter by multiplying by 100. An alternative method used for high-count samples was similar except that the 10 portions were taken from the entire mixed sample. The conversion to count-per-liter was obtained by multiplying the average by 1,000.

Copper

To determine the copper concentration, we used the method described by Hoste, Eeckhout, and Gillis (1953). This was preferred to that of Chow and Thompson (1952) because the latter method is not so selective for waters of variable pH, such as is found in the lagoon. Further, when coastal and bay waters are analyzed by this method, a turbid extract forms occasionally that is difficult to analyze.

Zooplankton

The zooplankton samples were obtained by pumping 250 gallons of water through a plankton net of No. 2 bolting silk. These were diluted to 100 ml., and an aliquot part checked for the various types of zooplankton. The count of each was recorded as count per 100 liters by multiplying by the appropriate factors. The size of the aliquot part varied, depending on the population density of the sample.

Barnacle setting rate

The barnacle attachment rate was based on the average daily setting-rate on 4-inch square cement plates suspended horizontally 2 feet below the surface at each station. The rate was estimated by averaging the count per square centimeter of eight locations on each plate, and then dividing by the number of days that the plate was submerged in the lagoon.

***Prorocentrum* sp.**

We used Wilson's (1959) dialysis membrane bag method for evaluating the effects of the copper ore on *Prorocentrum* sp. cultures suspended in the lagoon. Initial and final population estimates were made by counting the organisms in several 0.01 ml. portions taken immediately before the culture was placed in the dialysis bags and after their removal from the lagoon.

RESULTS

Chlorophyll

The results of the chlorophyll a, b, and c analyses are shown in figure 2. We have placed the November 1958 to April 1959 section of the graph under the corresponding months of 1957 and 1958 to simplify seasonal comparison. The phytoplankton blooms noted during November 1957 and January to March 1959 were reduced during the corresponding months of 1958 and 1959. Whether or not this was an effect of the ore is not known. The significant fact shown is the continued productivity of the lagoon after the addition of ore. This is indicated by the continuation of chlorophyll concentrations that are representative of a highly productive area (Zein-Eldin, 1959).

Salinity

Figure 3 shows monthly salinity ranges and averages of the lagoon. All data are based on the average of station salinity values.

Gymnodinium splendens

The average population of *G. splendens* in the lagoon from November 1957 to June 1959 is shown in figure 4. The November 1958 to June 1959 portion of the graph has been placed under the corresponding months of 1957 and 1958 to simplify a comparison of similar seasons. It can be seen that the seasonal occurrence has not been altered by the immersed ore. The January 1959 to April 1959 zero count cannot be considered significant as far as the copper ore experiment is concerned because of the subsequent rise that followed the pattern of the previous year.

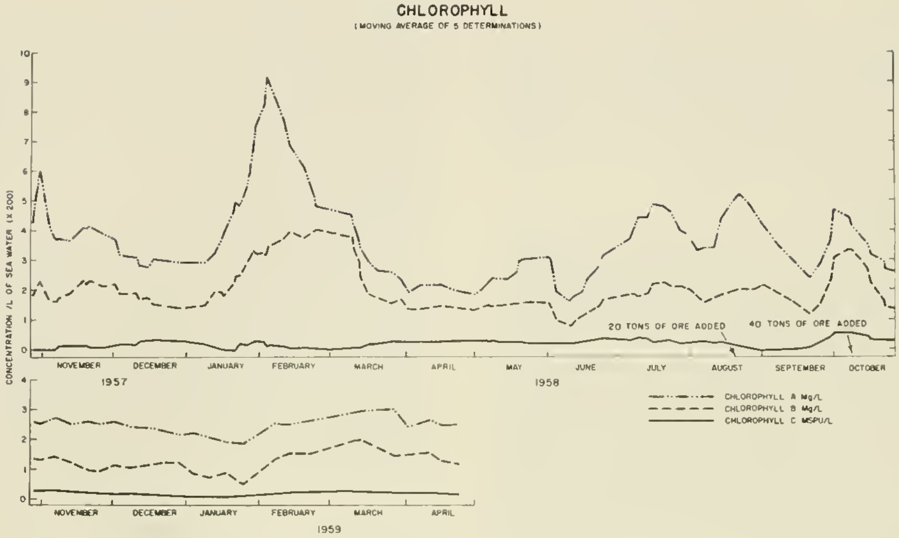

FIGURE 2.—Average chlorophyll concentration of East Lagoon from station samples.

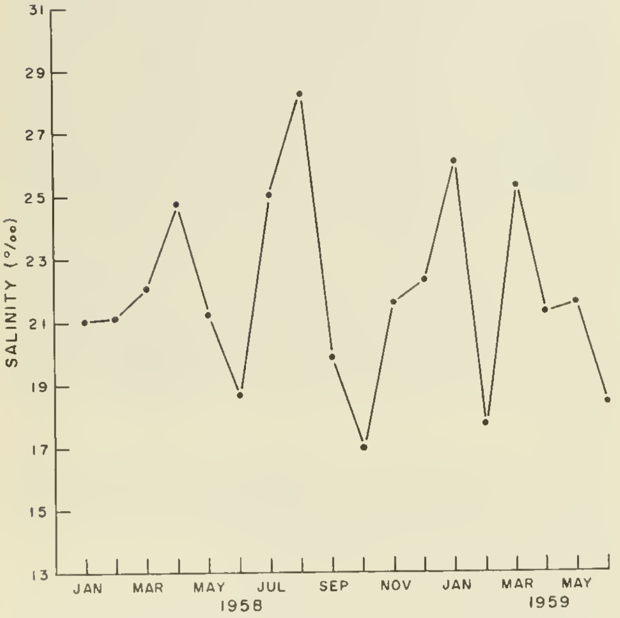

FIGURE 3.—Salinity of East Lagoon showing monthly averages.

Copper

Twenty tons of ore were added to the lagoon August 21, 1958. The effect of this addition on the overall copper concentration based on the average of station results is shown in figure 5. A maximum of 0.14 µg. at. Cu/l. was attained in less than a week but was reduced to the low value shown by the excessive tidal and drainage dilution that accompanied hurricane "Ella". The low maximum of 0.14 µg. at. /l. indicated that a second and larger addition would be necessary to obtain a copper concentration lethal to *G. breve*. Accordingly, on October 21 an additional 40 tons were

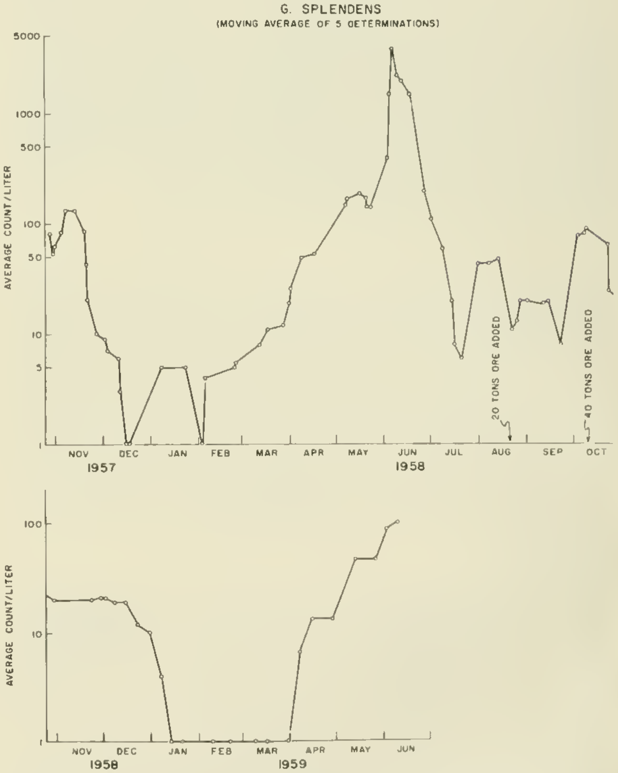

FIGURE 4.—*Gymnodinium splendens* (average counts for all stations).

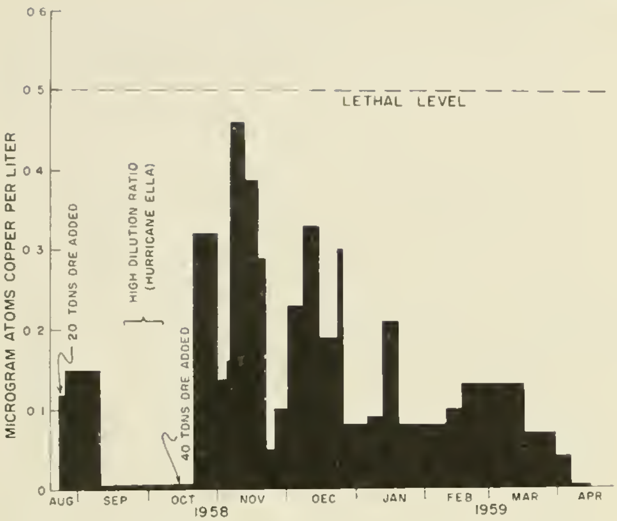

Figure 5.—Copper concentrations (average of all stations) showing approximate minimum lethal level from laboratory experiments.

placed in the lagoon. Again the results were disappointing. A near lethal concentration was attained but decreased during the next 5 months to about 0.01 µg.at./l. In some respects, the effects of the ore were similar to those of copper sulphate employed in the Florida red-tide control experiments (Rounsefell and Evans, 1958). The rapidly attained maximum levels soon decreased to normal values for the area. In the Florida control tests, however, lethal levels were reached, and the decline that followed occurred in a matter of days rather than months. Undoubtedly, variation in the hydrography and chemistry of the two areas accounted for much of the difference in maximum levels attained and also in the rates of decline. The water of the lagoon is high in particulate matter (fig. 6), and the copper from the ore was assumed to have been adsorbed and made unavailable by the muds, plankton organisms, and other material making up the particulate matter (Harvey, 1955).

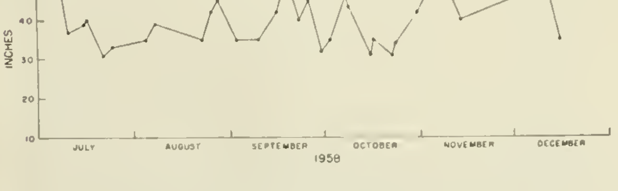

Figure 6.—Turbidity of East Lagoon. Average Secchi disk readings from stations.

Zooplankton

A qualitative and quantitative study of the standing crop of zooplankton in the lagoon was made by Fleminger (1959). The outstanding observation of his work was the broad summer-abundance peak and secondary peak combined with troughs in the early spring and autumn (fig. 7). Of particular significance is the January to March 1959 secondary peak which indicates continued growth of zooplankton populations following the addition of copper ore.

Barnacle setting rate

This study, conducted by Aldrich (1958a), showed that the adult barnacle population of the lagoon consisted almost exclusively of the brackish-water species, *Balanus eburneus*. Another brackish-water species found occasionally was *Balanus improvisus*. The data in figure 8 indicate the seasonal nature of barnacle setting in the lagoon. The outstanding feature is the continuance of the seasonal growth pattern after addition of the ore.

***Prorocentrum* sp.**

Table 1 shows the initial and final counts of *Prorocentrum* sp., and copper concentration of the cultures in the dialysis bags used in the lagoon. More than half of these cultures increased in population count. The data indicate that the greatest increase occurred in cultures having the lowest initial count. Presumably, these had not reached their peak when placed in the lagoon.

The copper concentration apparently did not interfere with the population growth of the organism. There was one exception: approximately 60 percent mortality occurred within the 4-day bags placed at station 4 on October 10. This was the day of the second ore addition (table 1), and the day that the greatest concentration of copper was observed within the bags.

Live car organisms

Laboratory experiments (Aldrich, 1958b) conducted in conjunction with the copper ore study indicated that the snail *Littorina irrorata* was probably most susceptible to copper poisoning. Twenty-four-hour tests demonstrated, however,

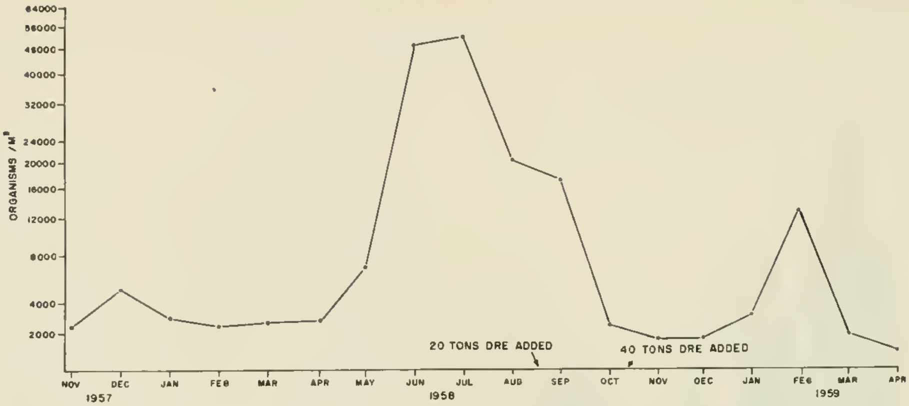

FIGURE 7.—Zooplankton concentration. Average of plankton samples taken at stations 1, 3, and 7.

TABLE 1.—Summary of dialysis bag data showing initial and final counts of organisms and final copper content of bags placed in East Lagoon, after addition of ore

Date	Days in lagoon	Count/.01 ml.		Copper µg.at./l.
		Initial	Final	
Aug. 23	4	43	43	0.19
25	2	21	50	.17
25	4	21	48	.18
27	2	52	39	.28
27	4	52	41	.24
29	2	48	42	.26
29	4	48	42	.21
Oct. 10	2	32	42	-----------
10	4	32	[1] 40	.41
12	2	35	36	.32
12	4	35	39	-----------
14	2	12	37	.12
14	4	12	26	.13
16	2	24	24	.25
16	4	24	26	.19
18	2	22	16	.20
18	4	22	25	.18

[1] About 60 percent of the organisms in the bags at Station 4 were dead.

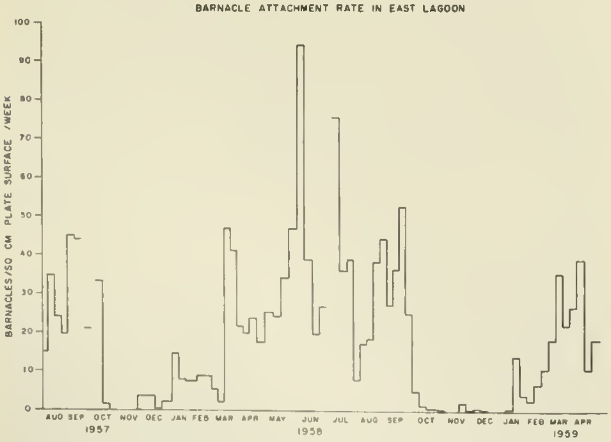

FIGURE 8.—Barnacle attachment in East Lagoon.

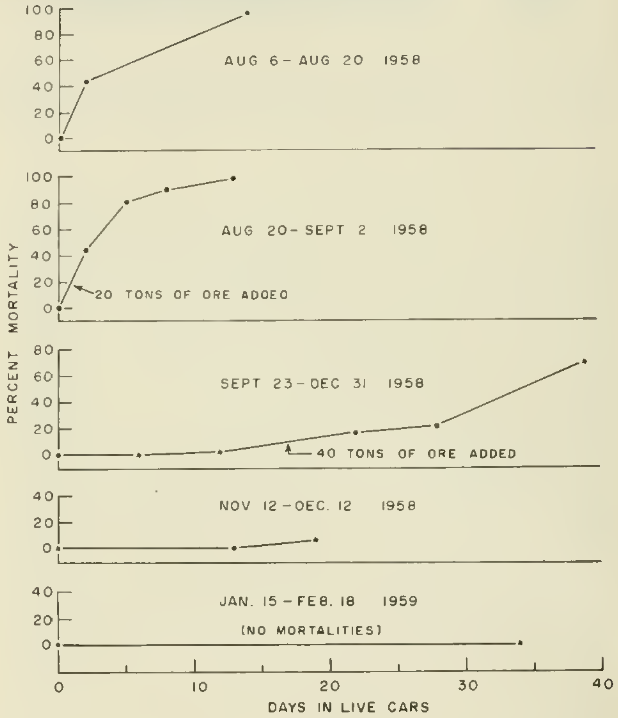

FIGURE 9.—Mortality of *Littorina irrorata* in East Lagoon.

that the snail could tolerate copper concentrations of 8 µg. at./l. with only temporary minor discomfort. The mortality rate of this organism for five test periods is shown in figure 9. The snails represented by the August 6 to September 2 periods were a generation older than those used in subsequent experiments. We believe increased age was the cause of greater mortality rate shown. The decrease in mortality following the addition of the copper ore indicates that the ore had little or no detrimental effect on this organism. The relatively small increase of the copper concentration in the lagoon apparently did not have a significant effect on the mortality rates of the other species in the live car.

DISCUSSION

Experiments conducted in our laboratories indicate that more copper ore is required to reach the toxic level for *Gymnodinium breve* in lagoon water than in Florida coastal water. This is thought to be due to the large amounts of natural chelators and particulate matter present in the lagoon as opposed to the relatively clear Florida waters. On the other hand, the Florida coastal waters receive more tidal flushing and dilution than the lagoon, and we would expect the maximum level of copper concentration to be less permanent than that shown for the lagoon in figure 5. Even assuming a toxic level could be reached in the Florida coastal waters, large quantities of ore would have to be added at frequent intervals which would make the cost prohibitive.

SUMMARY

An analysis of the biological and chemical data shows that the copper concentration of the lagoon was not increased to a level lethal to *Gymnodinium breve* after the addition of 60 tons of ore. The flora and fauna of the lagoon and organisms placed there in dialysis bags and live cars showed no significant effect attributable to the ore. The copper level, after the addition of the ore, increased to a maximum that was below the laboratory estimate of the level toxic to *G. breve* (based on Florida sea water) and then dropped to a lower level. These results show that the ore is not capable of maintaining a sufficiently high copper concentration to be considered as a means of controlling red tide outbreaks in waters similar in quality to that of the lagoon.

Results of this experiment indicate that copper ore does not have the desired characteristics of a red tide controlling agent, and we recommend that it not be used.

LITERATURE CITED

ALDRICH, DAVID V.
1958a. Barnacle attachment rates at Galveston, Texas. U.S. Department of the Interior, Fish and Wildlife Service, Annual Report of the Gulf Fishery Investigations for the year ending June 30, 1958, p. 89.
1958b. Toxicity of copper to marine organisms. U.S. Department of the Interior, Fish and Wildlife Service, Annual Report of the Gulf Fishery Investigations for the year ending June 30, 1958, p. 86.

CHOW, TSAIHWA J., and THOMAS G. THOMPSON.
1952. The determination and distribution of copper in sea water. Journal of Marine Research, vol. 11, No. 2, pp. 124–138.

CREITZ, GRACE I., and FRANCIS A. RICHARDS.
1955. The estimation and characterization of plankton populations by pigment analysis. III. A note on the use of "Millipore" membrane filters in the estimation of plankton pigments. Journal of Marine Research, vol. 14, No. 3, pp. 211–216.

DAVIS, CHARLES C.
1948. *Gymnodinium brevis* sp. nov. a cause of discolored water and animal mortality in the Gulf of Mexico. Botanical Gazette, vol. 109, No. 3, pp. 358–360.

FEINSTEIN, ANITA, A. RUSSELL CEURVELS, ROBERT F. HUTTON, and EDWARD SNOEK.
1955. Red tide outbreaks off the Florida west coast. Marine Laboratory, University of Miami, Report 55–15 to the Florida State Board of Conservation, 44 pp.

FLEMINGER, ABRAHAM.
1959. East Lagoon zooplankton. In Galveston Biological Laboratory fishery research for the year ending June 30, 1959. Bureau of Commercial Fisheries, U.S. Fish and Wildlife Service, Circular 62, pp. 114–118.

GATES, JEAN A., and WILLIAM B. WILSON.
1960. The toxicity of *Gonyaulax monilata* Howell to *Mugil cephalus*. Limnology and Oceanography, vol. 5, No. 2, pp. 171–174.

GUNTER, GORDON.
1942. Recurrent summer fish mortalities on the Texas coast. American Midland Naturalist, vol. 28, p. 631.

HARVEY, H. W.
1955. The chemistry and fertility of sea water. Cambridge, England, University Press, 224 pp.

HOSTE, J., J. EECKHOUT, and J. GILLIS.
1953. Spectrophotometric determination of copper with cuproine. Analytica Chimica Acta, vol. 9, pp. 263–274.

RICHARDS, FRANCIS A., with THOMAS G. THOMPSON.
1952. The estimation and characterization of plankton populations by pigment analyses. II. A spectrophotometric method for the estimation of plankton pigments. Journal of Marine Research, vol. 11, No. 2, pp. 156–172.

ROUNSEFELL, GEORGE A., and JOHN E. EVANS.
1958. Large-scale experimental test of copper sulphate as a control for the Florida red tide. U.S. Department of the Interior, Fish and Wildlife Service, Special Scientific Report—Fisheries No. 270, 57 pp.

WILSON, WILLIAM B.
1959. Evaluating toxicity of dissolved substances to microorganisms using dialysis membranes. In Galveston Biological Laboratory fishery research for the year ending June 30, 1959. Bureau of Commercial Fisheries, U.S. Fish and Wildlife Service, Circular 62, pp. 100–102.

ZEIN-ELDIN, ZOULA P.
1959. Plankton pigments in East Lagoon. In Galveston Biological Laboratory fishery research for the year ending June 30, 1959. Bureau of Commercial Fisheries, U.S. Fish and Wildlife Service, Circular 62, pp. 106–107.

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VALIDITY OF AGE DETERMINATION FROM SCALES OF MARKED AMERICAN SHAD

By Mayo H. Judy

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ABSTRACT

In the fall of 1952, one hundred thousand juvenile American shad, marked by removal of the right pelvic fin, were released in the Connecticut River. Seventeen marked fish were recovered in the river in 1956, 70 in 1957, and 39 in 1958. Ages of the fish, determined from their scales, were 4, 5, and 6 years, respectively. These findings were in agreement with known age established from marking and therefore validate annuli and spawning marks as criteria for age determination of shad.

VALIDITY OF AGE DETERMINATION FROM SCALES OF MARKED AMERICAN SHAD

By Mayo H. Judy, *Fishery Research Biologist*,
Bureau of Commercial Fisheries

In 1950, the U.S. Fish and Wildlife Service, as the primary research agency of the Atlantic States Marine Fisheries Commission, began a study of the American shad (*Alosa sapidissima*) on the Atlantic coast of the United States. Objectives of this investigation were to determine the causes for decline in the commercial yield from approximately 50 million pounds in 1896 to 8 million pounds in 1950, to determine conditions favoring recovery, and to provide information for scientific management of the fishery. A necessity for accomplishing these objectives was an accurate method of aging shad.

Prior to this investigation, techniques for aging shad had been presented by various workers. Leim (1924) determined age by means of winter rings or annuli on scales and established the relation between scale and body length. Borodin (1925) presented a method of reading scales by counting the number of transverse grooves and dividing by 2 to determine the age in years. Barney (1925) found evidence in otolith markings to indicate that age estimates as reported by Borodin were correct, but Greeley (1937) stated that Borodin's method gave misleading results. Greeley found that Leim's method of age determination agreed with the results of his studies on Hudson River shad.

Cating (1953) proposed a method for reading shad scales for total age, age at first spawning, and number of times the fish had previously spawned. Transverse groove counts were used to separate true from fasle annuli to the fourth annulus, and age of fish spawing for the first time was determined by counting the number of annuli and adding 1 year for the scale edge. Age of fish spawning for the second or more times was obtained by counting the number of annuli plus the number of spawning marks and adding 1 year for the scale edge.

Although Cating aged shad with apparent confidence he did not establish the validity of his readings. LaPointe (1958), using Cating's method, validated the annulus to be a true year mark on scales of fish spawning for the first time. He found that Leim mistook the fresh-water mark for the first annulus, thus causing a difference of 1 year between Leim's age determination and those in his study. Hammer (1942) confirmed that the fresh-water zone was a distinct and measurable scale growth formed while juveniles are in fresh water.

In 1952, prior to the completion of Cating's scale study, a marking program was conducted on juvenile shad in the Connecticut River. The objective of this program was to recover in future years marked fish of known age, thereby to check the method employed by Cating and to establish a correct method for aging shad from their scales. This was deemed necessary because techniques used prior to this time were subject to question.

Data presented in this paper were derived from the scales of marked adult shad recovered 4, 5, and 6 years following the marking program. Scales from these fish of known age were studied to determine the validity of annuli and spawning marks for age determination.

Appreciation is expressed to the Connecticut Power and Light Company for use of the Windsor Locks Canal System, and to the shad fishermen and fish dealers of the Connecticut River for their cooperation in this study.

LIFE HISTORY

Shad range on the Atlantic coast from the St. Johns River in Florida to the St. Lawrence River in Canada. It is an anadromous fish and spawning migrations begin as early as November in

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Florida and as late as June in Canada. The young remain in the rivers until fall, attaining lengths from 3 to 5 inches, then migrate to sea. Winters are probably spent off the Middle Atlantic, and summer and fall in the Gulf of Maine. After reaching maturity, in 3 to 6 years, they return to the rivers to spawn. Adult shad native to streams north of Cape Hatteras (N.C.) that survive spawning and other hazards return to the sea and re-enter the rivers to spawn again in successive years. Shad native to streams south of Cape Hatteras die after spawning (Talbot and Sykes, 1958).

MATERIALS AND METHODS

In the fall of 1952, 100,000 downstream migrant juvenile shad were marked on the Connecticut River in the Windsor Locks Canal, Windsor Locks, Conn. Marking of these fish, which averaged about 4 inches in fork length, was accomplished by clipping the right pelvic fin close to the body of the fish. Juveniles were trapped, seined, and marked in one level of the canal and then placed in a lower level of the canal and flushed into the main river. Samples of fish were held overnight to obtain an estimate of mortality. Mortality from marking was estimated at 30 percent; therefore, it was assumed that 70,000 marked juveniles were returned to the river.

The first marked fish were recaptured in the Connecticut River in 1956 from commercial catches and shad passed by the fishway at Hadley Falls Dam, Holyoke, Mass. Subsequent recoveries were made in 1957 and 1958 from commercial and sport catches. Approximately 35,000 shad were examined annually. From the 1956 collection it was determined that some shad had malformed, or naturally missing, pelvic fins. Therefore, in 1957, fish with various pelvic fin abnormalities were collected so that a wide assortment of abnormal fins would be available for comparison with marked fins. The pelvic girdle section of each fish collected was removed, labeled, and preserved. In addition, scale samples were taken and the length, weight, and sex recorded.

EXAMINATION OF SCALES

Two scales from each fish collected were impressed in plastic, using a modification of the method described by Greenbank and O'Donnell (1950). The scale impressions were read on an Eberbach projector, by two biologists using Cating's (1953) method for determining age of shad. Age readings were compared and the results confirmed.

In this method the scale edge is counted as a year mark because the last annulus (near scale periphery) is frequently eroded during the spawning migration. For example, a shad spawning for the first time (virgin fish) at 4 years of age has 3 annuli on the scale plus the scale edge for a total age of 4 years. After shad spawn and return to the sea, renewed feeding and resumption of growth leaves a characteristic scarlike mark on the scale edge where erosion occurred during the spawning migration (Moss, 1946). This is designated as a spawning mark and is used in place of the eroded annulus, formed prior to spawning, for determining age of "repeater" fish (those spawning for the second or more times). For example, a 6-year-old repeater spawning for the second time has 4 annuli and 1 spawning mark which, when read to include the scale edge, gives a total age of 6 years. The 4 annuli and 1 spawning mark indicate that this fish first spawned at 5 years of age and was on its second spawning run when captured.

EXAMINATION OF PELVIC FINS

Examination of the pelvic fin sections indicated that they contained malformed, missing, and marked fins. Malformed and missing fins are often found in fish as evidenced from studies by Cable (1956), Code (1950), and Rich and Holmes (1928). Marked fins were characterized by a varied pattern of fin regeneration ranging from no regeneration beyond formation of scar tissue to almost complete, but distorted regeneration. These findings are not unusual since, as reported by Stuart (1958), fin clipping seldom results in a uniform series of marks. From microscopic examination of regenerated marked fins, Stuart found that new growth of fin rays does not extend in a regular manner but commences as a thickened and undifferentiated cap, the connective and other tissues keeping pace with the growth of the adjacent rays. The degree and nature of fin regeneration was usually dependent on the angle of the cut and the amount of dermal-fin-ray tissue removed during clipping.

The pelvic fin section of each shad collected in

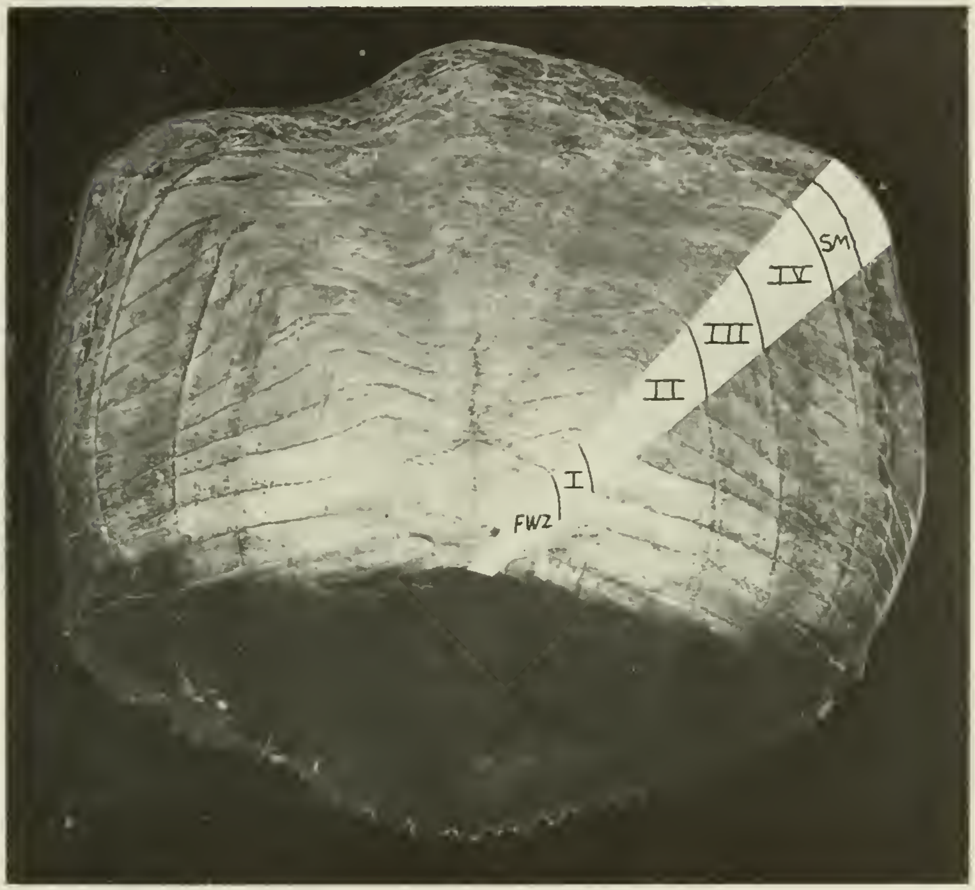

FIGURE 1.—Scale from 6-year-old shad spawning for the second time. (Roman numerals represent annuli, FWZ fresh-water zone, and SM spawning mark.)

this study was X-rayed using a method described by Sutherland (1958). Marked fins were identified from radiographs by an enlargement at the distal end of the radial bones extending partially or completely across the area of separation from the dermal fin rays (fig. 2). This method of classification of marked fish is in agreement with Stuart (1958) who found from microscopic examination that a palpable ridge was formed on marked fins at the site of cutting. Marked fins were classified according to the number of fin rays regenerated, regardless of the length of the rays, and placed in the following categories: (1) no regeneration—no fin rays; (2) one-third regeneration—one to three fin rays; (3) two-thirds regeneration—four to six fin rays; and (4) complete regeneration—seven to nine fin rays (fig. 2).

Pelvic-fin sections were classified as malformed if there was no enlargement at the distal end of the radials (fig. 3B, C). Missing fins were characterized by absence of radials or, in some specimens, absence of the entire pelvic girdle (fig. 3A, D), and absence of scar tissue at the site of fin origin. Malformed and missing fins were termed abnormal.

From a study of 28 shad collected in 1956, it was determined that 11 had abnormal pelvic fins. These included 4 males and 7 females of which 5 had malformed left or right pelvic fins and 6 had either the left, right, or both pelvic fins missing. These fish ranged in age from 3 to 6 years.

In 1957 fish with a variety of pelvic fin abnormalities were purposely collected. Of the 132 shad sampled, 62 were classified as abnormal.

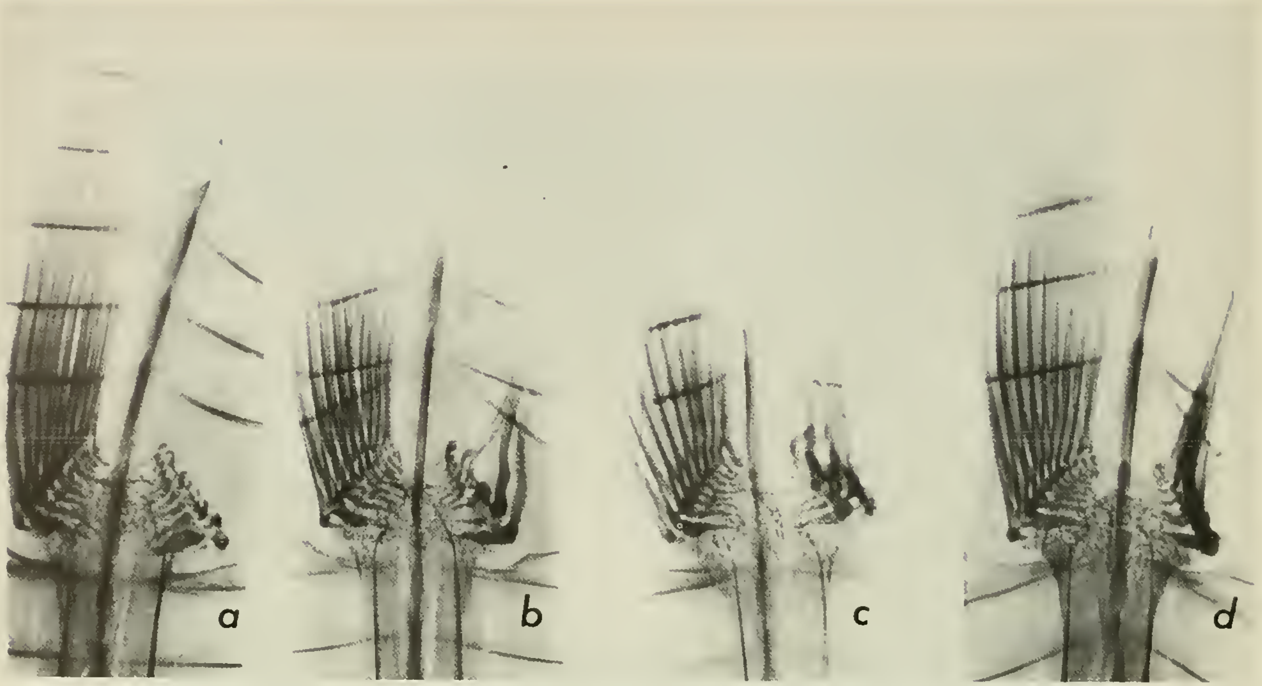

FIGURE 2.—Radiograph of pelvic fin sections from four marked shad. A—no regeneration, B—one-third, C—two-thirds, and D—complete regeneration.

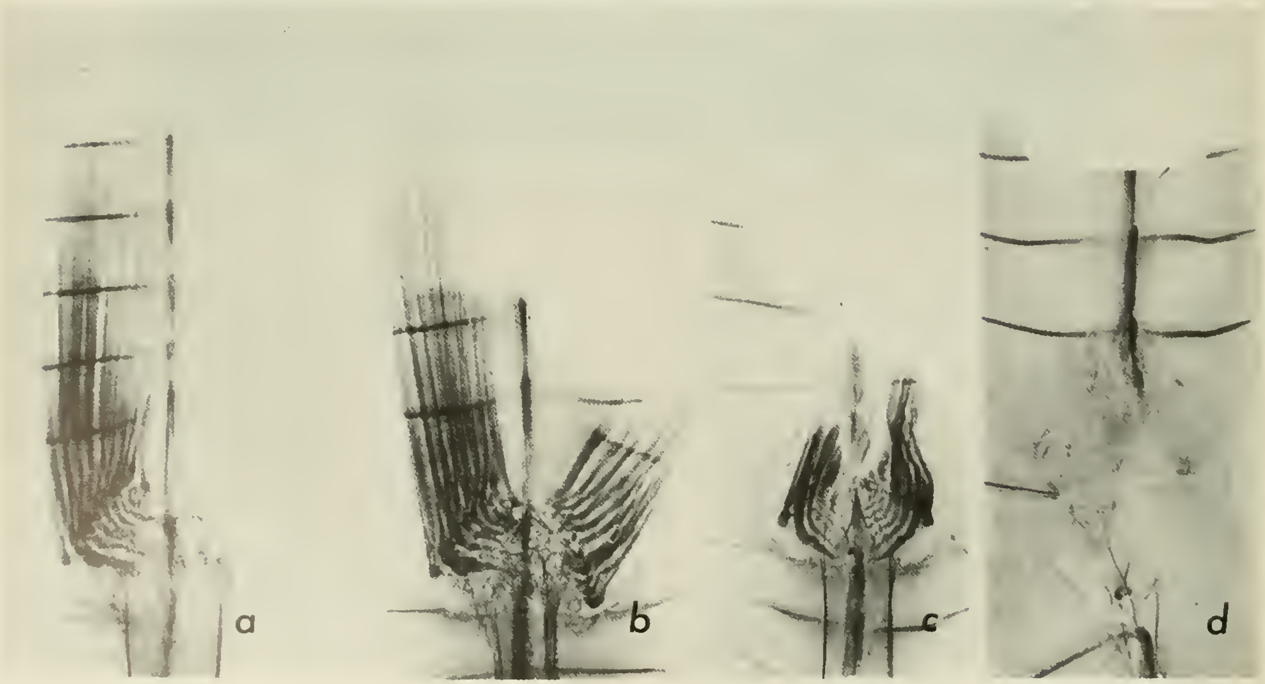

FIGURE 3. Radiograph of pelvic fin sections from four shad with malformed and missing fins (A—right fin and radial fin supports absent, B—right fin with malformed fin rays, C—double malformation of pelvic fins, and D—pelvic girdle absent.)

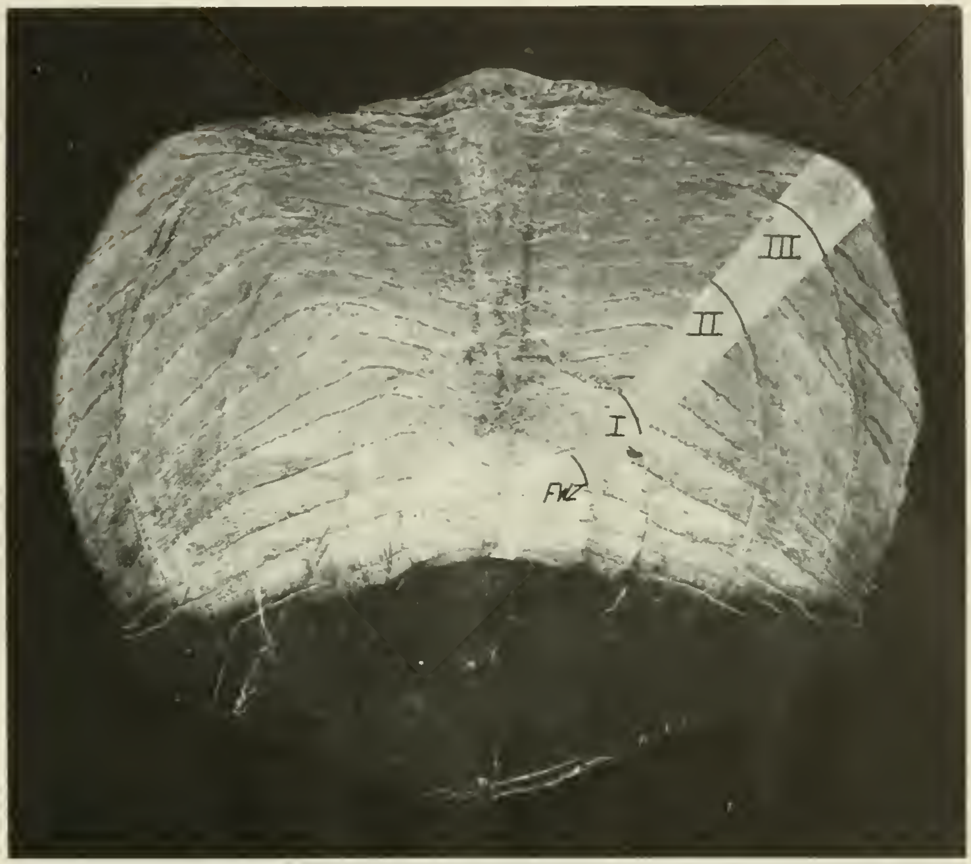

FIGURE 4.—Scale from 4-year-old marked shad spawning for the first time.

These included 21 males and 41 females of which 40 had either the left, right, or both pelvic fins malformed, and 22 had either the left, right, or both pelvic fins missing. These fish ranged in age from 4 to 7 years.

Of the 57 shad collected in 1958, 18 were classified as abnormal. These included 9 males and 9 females of which 6 had either the left, right, or both pelvic fins malformed and 12 had either the left, right, or both fins missing. These fish ranged in age from 4 to 8 years.

MARKED FISH RECOVERED 1956

From a study of pelvic fin sections and radiographs it was determined that 17 marked shad were recovered in 1956. These included 8 males and 9 females of which 3 had no regeneration of the right fin, 5 had one-third regeneration, 4 had two-thirds regeneration, and 5 had complete regeneration. Age readings indicated that all marked fish recovered were 4 years old, and spawning for the first time (fig. 4). Marked males averaged 16.4 inches, fork length, and 2.4 pounds in weight. Marked females averaged 17.9 inches, fork length, and 3.2 pounds in weight.

MARKED FISH RECOVERED 1957

From a study of pelvic fin sections and radiographs it was determined that 72 marked shad were recovered in 1957. Age determined from scale readings indicated that all but two of these fish were 5 years old. The ages of these two fish were 4 and 6 years. The radiographs and scale samples were re-examined and the above results confirmed. Therefore, on the basis of these findings, an error of approximately 3 percent exists either in interpretation of radiographs or in age determination.

The seventy 5-year-old fish that were marked included 14 males and 56 females of which 11 had no regeneration of the right pelvic fin, 18 had one-third regeneration, 26 had two-thirds re-

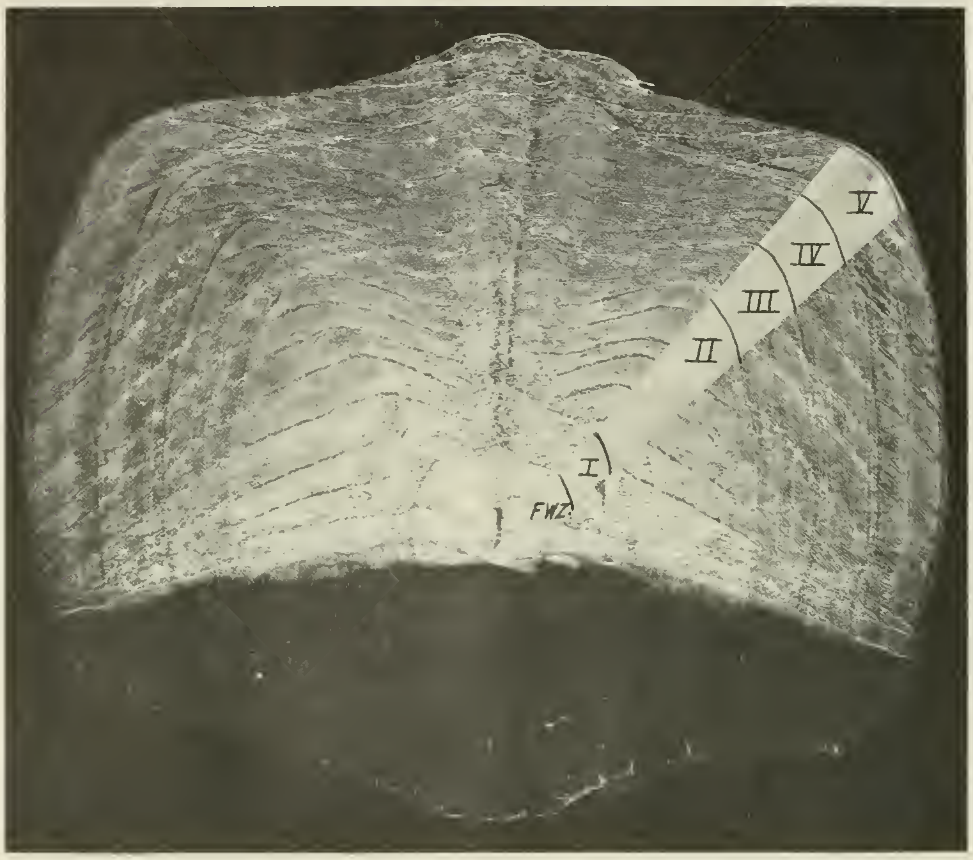

Figure 5.—Scale from 5-year-old marked shad spawning for the first time.

generation, and 15 had complete regeneration. This group consisted of 56 first- and 14 second-year spawners. Forty-three percent (6) of the males and 14 percent (8) of the females were spawning for the second time. Figures 5 and 6 illustrate representative scales from 5-year-old marked fish spawning for the first and second time. In figure 5 the fifth or last annulus is plainly visible, but since it was laid down just prior to the spawning migration, it is combined with the scale edge and counted as one year. Fish spawning for the second time (fig. 6) had first spawned in 1956 when 4 years old. Marked males averaged 17.6 inches fork length and 3.2 pounds in weight. Marked females averaged 18.8 inches, fork length, and 4.1 pounds in weight.

MARKED FISH RECOVERED 1958

From a study of pelvic fin sections and radiographs it was determined that 40 marked shad were recovered in 1958. Age determined from scale readings indicated that 39 fish were 6 years old and one was 5 years old. The radiographs and scale samples were re-examined and the above findings confirmed. Therefore, an error of approximately 2 percent exists either in interpretation of radiographs or in age determination.

The 39 marked recoveries included 16 males and 23 females, of which 11 had no regeneration of the right fin, 9 had one-third regeneration, 10 had two-thirds regeneration, and 9 had complete regeneration. This group consisted of 13 first-, 18 second-, and 8 third-year spawners. All males (16) and 43 percent (10) of the females had previously spawned. Sixty-two percent (10) of the males and 35 percent (8) of the females were spawning for the second year, and 38 percent (6) of the males and 9 percent (2) of the females were spawning for the third year. Figures 7 and 8 are representative scales from 6-year-old marked

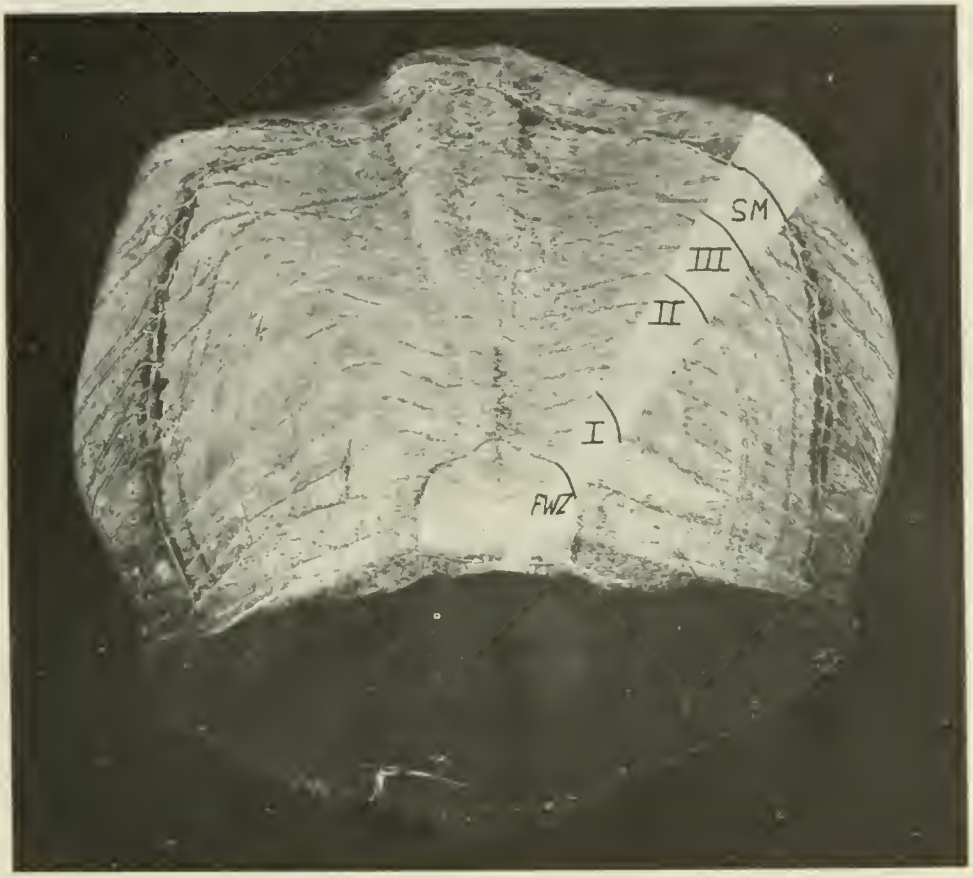

FIGURE 6.—Scale from 5-year-old marked shad spawning for the second time.

fish spawning for the first and third times.[1] Those spawning for the third time had first spawned in 1956 when 4 years old. The second spawning mark was laid down in 1957. Marked males averaged 18.2 inches fork length and 3.6 pounds in weight. Marked females averaged 19.1 inches fork length and 4.5 pounds in weight.

DISCUSSION AND CONCLUSION

Of the 129 fish classified from radiographs as marked, only 3 were in disagreement with age as determined from scale readings. These misclassifications, 2 in 1957 and 1 in 1958, were caused by error either in age determination or in interpretation of radiographs, which in some cases were difficult to interpret. This minor disagreement, approximately 2 percent of the fish classified as marked, was considered insignificant and in no way invalidates the findings of this report.

Methods used by Leim (1924), Borodin (1925), Greeley (1937), and Cating (1953), to age shad were all considered in this study. Of these methods, only Cating's proved to be a complete and valid means for determining total age, age at first spawning, and number of times previously spawned. LaPointe (1958) correctly validated the annulus as a true year mark on scales of shad spawning for the first time and he showed that Leim had mistaken the fresh-water mark for the first annulus. Therefore, the techniques used by Leim and Greeley to age shad gave age assessment 1 year greater than the actual age of the fish. Borodin's method, applied to scales of marked shad, gave erroneous results and could not be justified on the basis of the present study.

Age of marked fish collected in 1956, 1957, and 1958 as determined from scale readings, was in

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[1] Figure 1 is a representative scale from a 6-year-old marked shad spawning for the second time. These fish had first spawned in 1957 when 5 years old.

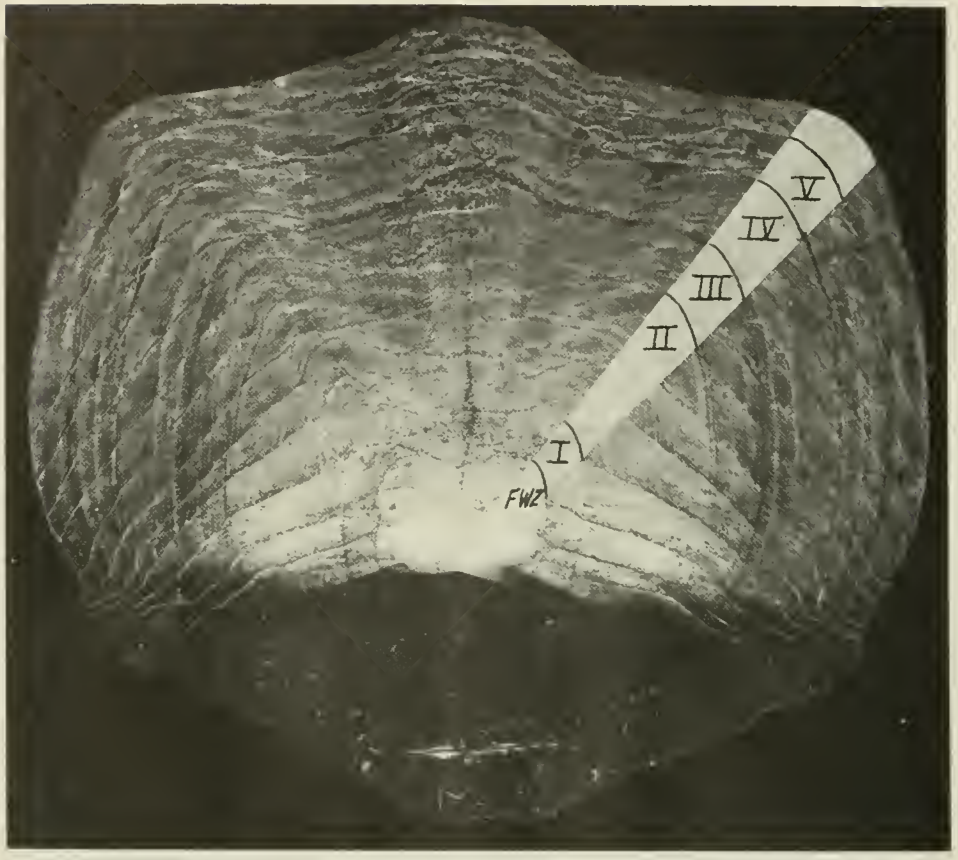

FIGURE 7.—Scale from 6-year-old marked shad spawning for the first time.

agreement with known age established by marking. These findings indicate that the method used to age shad (Cating, 1953) is valid and that annuli and spawning marks are true indicators of age.

SUMMARY

One hundred thousand juvenile shad from the Connecticut River were marked by removal of the right pelvic fin, in 1952. The objective of this program was to recover marked fish of known age in future years, to validate the use of annuli and spawning marks for determining age of shad.

Marked fish were first recovered in the Connecticut River in 1956 with subsequent recoveries in 1957 and 1958. Fish with marked and abnormal fins were collected in each of these years. Twenty-eight were collected in 1956, 132 in 1957, and 57 in 1958.

The pelvic fin section from each fish sampled was X-rayed and classified as follows: (1) marked, (2) malformed, and (3) missing. Marked fins were identified by an enlargement at the distal end of the radial bones at the point of separation from the dermal fin rays. Pelvic fin sections were classified as malformed, when there was no enlargement of the distal end of the radials. Missing fins were classified as to the fin or fins affected. The number of marked fish collected each year was determined from a study of pelvic fin sections and radiographs.

Scales from sampled shad were read for total age and number of times each fish had previously spawned. The 1956 recoveries of marked shad were 4-year-old fish spawning for the first time. Those collected in 1957 were 5-year-old fish, with recoveries divided between first and second year spawners. Fish spawning for the second time had first spawned in 1956. Marked fish collected in 1958 were 6 years old and consisted of first-, second-, and third-year spawners. Those spawning

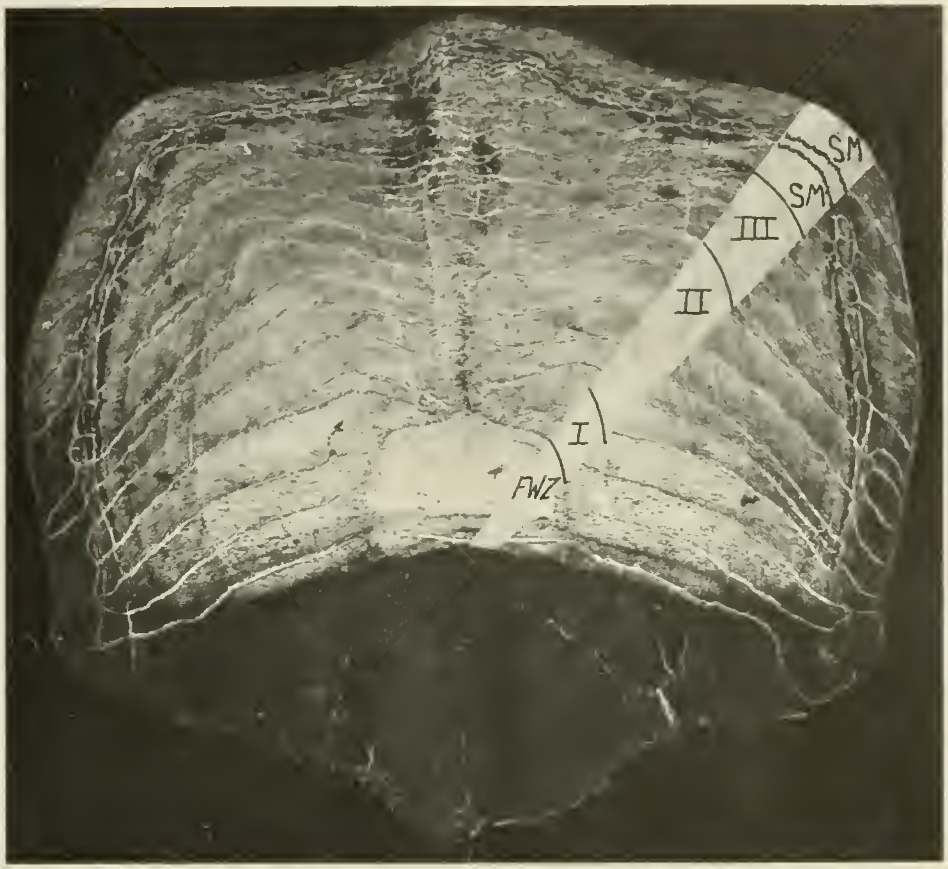

Figure 8.—Scale from 6-year-old marked shad spawning for the third time.

for the second time had first spawned in 1957, and those spawning for the third time had first spawned in 1956.

Age of marked shad, as determined from scale readings, was in agreement with known age established by marking. These findings validate the use of annuli and spawning marks for determining total age of shad.

LITERATURE CITED

Barney, R. L.

1925. A confirmation of Borodin's scale method of age determination of Conecticut River shad. In Mitchell, P. H., A report of investigations concerning shad in the rivers of Connecticut, Part III, pp. 52–60. Hartford, Conn.

Borodin, N. A.

1925. Age of shad *Alsoa sapidissima* (Wilson), as determined by the scales. In Mitchell, P. H., A report of investigations concerning shad in the rivers of Connecticut, Part II, pp. 46–51. Hartford, Conn.

Cable, Louella E.

1956. Validity of age determination from scales, and growth of marked Lake Michigan lake trout. U.S. Fish and Wildlife Service, Fishery Bulletin, No. 107, vol. 57, pp. 1–59.

Cating, James P.

1953. Determining age of Atlantic shad from their scales. U.S. Fish and Wildlife Service, Fishery Bulletin, No. 85, vol. 54, pp. 187–199.

Code, Mark R.

1950. Cutthroat trout without dorsal fins. Progressive Fish Culturist, vol. 12 (2): pp. 85–86.

Greeley, John R.

1937. Fishes of the area with annotated list. In New York Conservation Department: A biological survey of the lower Hudson watershed; supplemental to twenty-sixth annual report, 1936. Part II, pp. 45–103. J. B. Lyon Company, Albany, N.Y.

Greenbank, John, and D. John O'Donnell.

1950. Hydraulic presses for making impressions on fish scales. American Fisheries Society, Transactions, vol. 78 (1948), pp. 32–37.

Hammer, Ralph Curtis.

1942. The homing instinct of the Chesapeake Bay shad *Alosa sapidissima* (Wilson), as revealed by a study of their scales. Thesis, University of Maryland. 45 pp. (typewritten).

LaPointe, Donald F.
1958. Age and growth of the American shad, from three Atlantic coast rivers. American Fisheries Society, Transactions, vol. 87 (1957), pp. 139–150.

Leim, A. H.
1924. The life history of the shad *Alosa sapidissima* (Wilson), with special reference to the factors limiting its abundance. Biological Board of Canada, Contributions to Canadian Biology, vol. 2 (new series), No. 11, pp. 161–284.

Moss, Douglas D.
1946. Preliminary studies of the shad (*Alosa sapidissima*) catch in lower Connecticut River, 1944. Eleventh North American Wildlife Conference, Transactions, pp. 230–239.

Rich, W. H., and H. B. Holmes.
1928. Experiments in marking young chinook salmon on the Columbia River, 1916 to 1927. U.S. Bureau of Fisheries, Bulletin, vol. 44, pp. 215–264.

Stuart, T. A.
1958. Marking and regeneration of fins. Scottish Home Department, Freshwater and Salmon Fisheries Research, No. 22, pp. 1–14.

Sutherland, Doyle F.
1958. Use of diagnostic X-ray for determining vertebral numbers of fish. U.S. Fish and Wildlife Service, Special Scientific Report—Fisheries No. 244, 9 pp.

Talbot, Gerald B., and James E. Sykes.
1958. Atlantic coast migrations of American shad. U.S. Fish and Wildlife Service, Fishery Bulletin, No. 142, vol. 58, pp. 473–490.

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CALANOID COPEPODS FROM EQUATORIAL WATERS OF THE PACIFIC OCEAN

By GEORGE D. GRICE

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ABSTRACT

A systematic study was made of the calanoid copepods found in 14 zooplankton samples, four of which were obtained from within the recently discovered equatorial undercurrent (Cromwell current), collected between 5° N. and 5° S. and 130° E. and 120° W.

One hundred and ten species belonging to 18 families were recorded. Descriptive notes, measurements and figures were given for most species with citations to previous occurrences in the Pacific Ocean.

Except for *Scolecithricella tenuiserrata* (Giesbrecht), the copepod species in samples collected from within the equatorial undercurrent were not very different from those in samples obtained adjacent to the current. The numerical abundance and species diversity in equatorial waters were briefly compared with that reported for the northwestern Pacific Ocean. *Acrocalanus andersoni* Bowman, *Chirundina indica* Sewell and *Haloptilus fertilis* (Giesbrecht) were reported for the first time from the Pacific Ocean.

Three species, *Xanthocalanus dilatus, Amallophora smithae* and *Scolecithricella tropica,* are described as new, and hitherto unknown males of *Gaetanus miles* Giesbrecht and *G. minor* Farran are briefly illustrated from juvenile specimens. It was proposed that *Euchirella brevis* Sars is a synonym for *E. amoena* Giesbrecht; *Euchaeta consimilis* Farran for *E. concinna* Dana; *Scoecithrix longicornis* Scott, and *Scolecithricella spinipedata* Mori for *Scolecithricella ctenopus* (Giesbrecht); and *Centropages pacificus* Chiba for *C. elongatus* Giesbrecht.

CALANOID COPEPODS FROM EQUATORIAL WATERS OF THE PACIFIC OCEAN

By George D. Grice, *Woods Hole Oceanographic Institution* [1]

The present paper concerns the calanoid copepods found in plankton samples collected along the equator, an area which has been relatively unexplored taxonomically.

Systematic studies on calanoid copepods have made these microcrustaceans one of the better known groups of the holoplankton of the Pacific Ocean. Extensive taxonomic reports are available for the north Pacific (Brodsky, 1950), the northeast Pacific (Davis, 1949), the western Pacific (Vervoort, 1946; Tanaka, 1953), and the Pacific sector of the Antarctic (Vervoort, 1957). In addition there are numerous smaller but nevertheless valuable papers concerning the calanoid copepods of more restricted areas. Although there remain large, unexplored areas, these recent papers and certain of the older ones (e.g., Scott, 1909) provide a framework for a zoogeographic study of Pacific calanoids and, moreover, show where additional investigations are needed.

Most of the laboratory work of this study was done in Honolulu, Hawaii, in 1958 and 1959 under a fellowship from the John Simon Guggenheim Memorial Foundation. I wish to express my appreciation to the Foundation for the opportunity to make this study. The U.S. Fish and Wildlife Biological Laboratory furnished space for the work, the use of their library facilities and a part of their extensive plankton collections. It is a pleasure to acknowledge the cooperation of Thomas S. Aus-

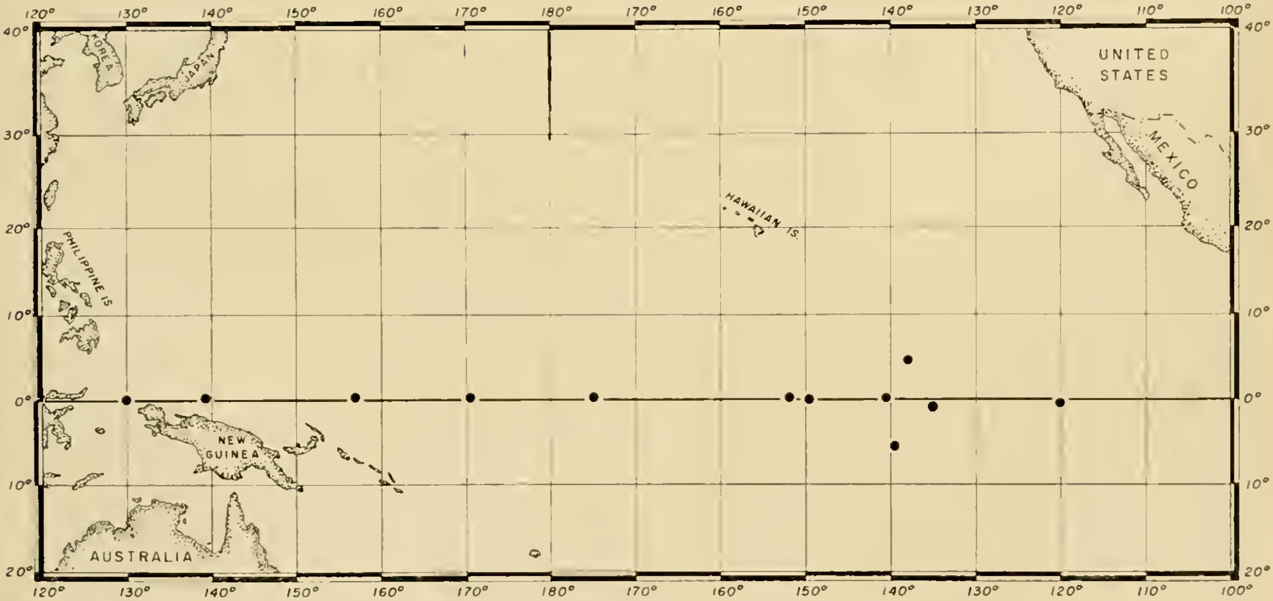

FIGURE 1. Positions where plankton samples were obtained.

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[1] Woods Hole, Mass.

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tin and E. C. Jones. I wish also to thank Dr. Paul Illg for his advice during the course of the work, Dr. Thomas E. Bowman for reviewing the manuscript, and my wife, Joan, for assistance in completing the drawings.

MATERIALS

The present report is based on the examination of 14 plankton samples collected between 5° N. and 5° S. latitude and between 130° E. and 120° W. longitude in the Pacific Ocean (fig. 1). The pertinent data associated with each plankton collection are presented in table 1. Hydrographic data associated with these collections are given by King, Austin, and Doty (1957) for the research vessel *Hugh M. Smith*, cruise 31, and by Austin (1957) for cruise 35. Processed reports containing hydrographic data have been issued for *Orsom* cruise 56–4 (Legand, 1957), for *Stranger* and *Horizon* cruises (Scripps Institution of Oceanography, 1957), and for *Satsuma* and *Kagoshima* cruises (Japanese Hydrographic Office, 1956).

Four of the 14 samples (*Smith* cruise 31, stations 94, 144, 178, and cruise 47, station 31) were obtained from the recently discovered equatorial undercurrent (Knauss and King, 1958) by means of closing net gear. In addition, one oblique tow (*Smith* cruise 35, station 63) apparently passed within the undercurrent at least during part of the tow.

The three samples obtained on cruise 47 were oriented with respect to the undercurrent. One sample (cruise 47, station 31) was collected within the current, and the other two were obtained from below it (cruise 47, station 29) and from above it (cruise 47, station 30).

Six collections (*Smith* cruise 35, station 63, *Stranger* 34, *Orsom* 10, *Horizon* 32, *Satsuma* 32, and *Kagoshima* 613) were selected from a large number of plankton samples obtained by vessels participating in a large scale quasi-synoptic study (Operation Equapac) in Pacific equatorial waters. The samples used in the present studies are those obtained nearest to the Equator by each of the vessels.

METHODS

Owing to the large volume of most of the samples, except *Kagoshima* 613, it was not practical to examine the entire contents of each. In order to estimate the percentage representation and the numerical abundance of the common species, small quantities of the original samples were examined. These sub-samples, the sizes of which are given in table 2, were obtained by means of a plankton splitter (McEwen, Johnson, and Folsom, 1954). On

TABLE 1.—*Plankton station data*

Research vessel	Agency	Cruise No.	Station No.	Position	Date	Time[1]	Size of net	Mesh (mm.)	Depth [2] (m.)	Water filtered (m.^{3})
Hugh M. Smith	U.S. Fish and Wildlife Service.	31	94–2	00°11′S 119°58′W	*1955* Nov. 7	0916–0946 ZT	1 m.	0.65	146–72 CN	590.2
Do	do	31	132–2	04°40′N 138°14′W	Nov. 17	0921–0950 ZT	1 m.	65	119–63 CN	690.8
Do	do	31	144–2	00°16′N 140°12′W	Nov. 20	1000–1036 ZT	1 m.	.65	122–61 CN	38.0
Do	do	31	153–3	05°31′S 139°54′W	Nov. 22	1008–1039 ZT	1 m.	.65	126–63 CN	966.4
Do	do	31	178–2	00°21′N 151°40′W	Dec. 6	0917–0947 ZT	1 m.	.65	146–68 CN	283.8
Do	do	47	30	00°00′ 149°36′W	*1958* Oct. 27	1118–1151 ZT	1 m.	.65	surface	1342.0
Do	do	47	31	00°00′ 149°33′W	do	1153–1246 ZT	1 m.	65	100 CN	380.0
Do	do	47	29	00°00′ 149°38′W	do	0953–1112 ZT	1 m.	.65	500 CN	922.0
Do	do	35	63–1	01°10′S 134°57′W	*1956* Aug. 19	2116–2152 ZT	1 m.	66	169 Q	
Stranger	Scripps Institution of Oceanography.		34	00°01′N 174°59′W	Sept. 15	0352 GMT	1 m.	.56	0–140 Q	
Orsom	Institut Français d'Océanie.	56–4	10	00°35′N 170°11′E	Oct. 4	2338–2457 LT	50 cm.	.366	150 Q( )	616.0
Horizon	Scripps Institution of Oceanography		32	00°03′S 157°00′E	Aug. 25	0428 GMT	1 m.	56	0–280 Q	
Satsuma	Japan Hydrographic Office.		32	00°29′N 139°49′E	Aug. 18	2100–2210 ZT	45 cm.	33	0–150 Q	20.71
Kagoshima-Maru	Kagoshima University, Japan.		613	00°38′N 130°20′E	Aug. 1	0725–0955 ZT	22.5 cm.	.11	0–50 V	

[1] ZT, zone time; LT, local time; GMT, Greenwich mean time.
[2] CN, closing net; Q, oblique open net; V, vertical open net.

TABLE 2.—*List of species and number of specimens in each sub-sample*

["X" indicates the species was found during the examination of other fractions of original sample]

Species	*Hugh M. Smith*									*Stranger*	*Orsom*	*Horizon*	*Satsuma*	*Kagoshima*
	94	132	144	153	178	30	31	29	63	34	10	32	32	613
1. Calanus tenuicornis	2	1		3	2							1		
2. Nannocalanus minor	1	44	2	21	41		2	X	2	6	6	12		
3. Canthocalanus pauper									1	1		2		
4. Neocalanus gracilis	X	8		6			17			X	X		X	
5. N. robustior				1	X				1	X				
6. Undinula vulgaris													X	
7. U. darwini	1	1	4	72	57	20	11	X	39	6	2	11	6	
8. Eucalanus attenuatus		1		15	4	1	15		15	X		11		
9. E. mucronatus												2		
10. E. subtenuis	1	85	86	2	173		39		45					
11. E. pileatus													1	
12. E. subcrassus									3	X	4			
13. Rhincalanus cornutus	X		1	1			3	48	9	1	2	1	5	
14. R. nasutus	1													
15. Paracalanus aculeatus			X	3	3		1		11	3	4	1		
16. P. parvus	X													
17. P. dubia														1
18. Acrocalanus longicornis				2			1		1	X				
19. A. andersoni										1	X			1
20. A. monachus										X	X	3		
21. Calocalanus pavo				1					1	1	1	X		
22. C. plumulosus													X	
23. Clausocalanus arcuicornis	3	75	4	9	27	15	11		3	12	18	9	5	
24. C. furcatus		30		14	3		1		6	6		4	1	
25. Euaetideus giesbrechti	1		1					X	X					
26. E. acutus	5	2	3	X	11	X	4		X	X				
27. E. bradyi	13		3						X					
28. Chiridius poppei	2								X					
29. Gaetanus miles								2	X					
30. G. minor								6	3			X		
31. Euchirella bella				X			X		X	X				
32. E. venusta									X					
33. E. pulchra									X					
34. E. amoena		X	X	X	X				X					
35. E. curticauda											X			
36. E. maxima								X						
37. Pseudochirella sp.								X						
38. Chirundina streetsi												X		
39. C. indica									X					
40. Undeuchaeta plumosa									X			X	1	
41. U. intermedia									1			X		
42. Euchaeta marina		1	X	33	8	34	12		7	5	X	2		
43. E. wolfendeni		1							1	5		4	2	
44. E. media									1					
45. E. tenuis								1	1			X		
46. E. concinna													4	
47. E. longicornis	2	4												
48. E. spinosa								X						
49. Phaenna spinifera	3	X					X		1		X	X		
50. Xanthocalanus dilatus n. sp.			X											
51. Amallophora smithae n. sp.			X											
52. Scolecithrix danae		2	4	18	5	X	26	X	17	3	1	7	6	
53. S. bradyi	14	4	X		1		1							
54. Scolecithricella ctenopus	1				1					1	X			
55. S. abyssalis	8		X					1	1					
56. S. vittata	4													
57. S. tenuiserrata			6		9		2		1	2				
58. S. marginata			X		X									
59. S. tropica n. sp.	4	4			2									
60. S. sp.			X											
61. Scaphocalanus echinatus									X					
62. S. longifurca	1							X	1					
63. Scottocalanus securifrons												X		
64. S. farrani								X						
65. S. sedatus								X			X			
66. Temoropia mayumbaensis	X										X			
67. Metridia venusta			7											
68. Pleuromamma xiphias									X		X		1	
69. P. abdominalis	2							13	7		X	1	5	
70. P. indica													1	
71. P. quadrungulata								5	X					
72. P. gracilis	1							12	X			1	X	
73. P. borealis									X		X		1	
74. Centropages gracilis		1		X	X	7				X			X	
75. C. elongatus				X								X	X	
76. C. calaninus						X						1		
77. Lucicutia flavicornis	15	3	X		11		3	X		1			1	
78. L. ovalis		X		1	4				X	2	1	1		
79. Heterorhabdus spinifrons			2					3	1				X	
80. H. papilliger	5	6	10		27		9	1	1	X	X			
81. Haloptilus longicornis	19	12	43	X	26		50		1	X	1	X	13	
82. H. acutifrons	X													
83. H. fertilis												X		
84. H. ornatus									X					
85. H. spiniceps	X									X	X	X	X	
86. H. austini	1													
87. Augaptilus longicaudatus	X													
88. Euaugaptilus hecticus							2			X			X	

TABLE 2.—*List of species and number of specimens in each sub-sample*—Continued

["X" indicates the species was found during the examination of other fractions of original sample]

Species	*Hugh M. Smith*									*Stranger*	*Orsom*	*Horizon*	*Satsuma*	*Kagoshima*
	94	132	144	153	178	30	31	29	63	34	10	32	32	613
89. Arietellus setosus									X					
90. A. giesbrechti								X						
91. A. plumifer	1								X					
92. A. aculeatus									X					
93. Candacia longimana												X	X	
94. C. guggenheimi								X						
95. C. tenuimana								X						
96. C. aethiopica						X						X	X	
97. C. pachydactyla		X		X	X	X			1	X	X	X		
98. C. curta								X			X	X		
99. C. bipinnata			X		X									
100. C. varicans							1		X					
101. C. catula					X				1	X	X	X		
102. C. bispinosa				3	X					X	X		1	
103. C. simplex	X	5	X	X	1									
104. C. truncata		X		1		X			X	1	X	8	15	
105. Pontella securifer						X	X							
106. P. tenuiremis												X		
107. Labidocera detruncata						X						X		
108. Pontellina plumata		X			X	7	X		X	1	X	1		
109. Acartia danae	1	1			X									
110. A. negligens				2	2	70	5		X	X	27		X	
Unidentified copepodids	22	70	18	5	22	0	0	41	44	30	2	23	28	5
Number of specimens in sub-sample	134	361	194	213	440	154	216	133	228	88	67	106	97	7
Sub-sample size	1/16	1/64	1/8	1/256	1/16	1/32	1/4	1/64	1/512	1/256	1/256	1/256	1/2	all
Number of copepods per cubic meter	3.6	33.4	40.8	56.4	24.8	3.7	2.3	9.2			27.8		9.3	
Number of species	34	27	26	27	31	15	25	25	55	35	31	39	29	2

completing the analysis of the sub-sample, portions of the original sample were examined for species not found in the aliquot. The species in each sample are listed in table 2 along with the number of specimens of each found in the aliquot.

Representatives of most species from each station were segregated by sex and placed in labeled vials. This material will be deposited in the U.S. National Museum.

GENERAL REMARKS

Species composition

A total of 110 species of calanoid copepods was found in the samples (table 2). Of these, three species belonging to the genera *Xanthocalanus, Amallophora,* and *Scolecithricella* are described as new, and three species, *Acrocalanus andersoni, Chirundina indica,* and *Haloptilus fertilis,* are reported for the first time from the Pacific Ocean.

The collections examined were obtained from along the Equator from 120° W. to 130° E., a distance of approximately 5,800 miles (fig. 1). Many of the species were widely distributed and occurred in samples collected in the eastern Pacific (east of 170° W.) and those collected in the western Pacific (west of 170° W.). Disregarding the small collection made at *Kagoshima* station 613, the most frequently occurring species were *Nannocalanus minor, Undinula darwini, Clausocalanus arcuicornis,* and *Scolecithrix danae.* These four species were present in all but one or two samples.

A study of table 2 will reveal that there were at least 6 species which were frequently found (4 or more samples) in the eastern Pacific, but which were not found in the samples examined from the western Pacific. One of these, *Eucalanus subtenuis,* was the most abundant copepod in three of the eastern Pacific samples and its apparent absence from the western Pacific samples is noteworthy. It is not, however, restricted to the eastern Pacific, as it has been reported from Japan (Fukase, 1957; Tanaka, 1956a) and from the Dutch East Indies (Vervoort, 1946). The other eastern Pacific species have also been reported from these two areas.

Equatorial undercurrent samples

Four of the fourteen samples examined were obtained from within the equatorial current (*Smith* 94, 144, 178, 31). The species composition of these samples, when compared with samples collected from adjacent waters—north (*Smith* 132), south (*Smith* 153), and above (*Smith* 30) and below (*Smith* 29) the undercurrent—was not particularly distinctive. *Scolecithricella tenuiserrata,* although apparently absent from one undercurrent sample (*Smith* 94), did appear in the other three samples and also in two other samples (*Smith* 63, *Stranger* 34) that were collected from depths where the undercurrent could be located, if present, but several hundred miles west of its known limits. Knauss (1959), has indicated that the current may extend as far west as about 160° E.; in that event the above two samples could have been collected from the current. Even if *S. tenuiserrata* is typically found within the undercurrent, it cannot be considered as an "indicator" *sensu stricto* of the current. In addition to the present samples, this species has been reported from near the Great Barrier Reef (Farran, 1936) and from Japan (Tanaka, 1953).

Numerical abundance

The number of copepods calculated for those collections in which a current meter was employed, varied from 2.3 to 56.4 with a mean of 21.8 copepods per cubic meter (table 2). These data may be compared to numerical data presented by Brodsky (1952) for the northwestern Pacific Ocean. Using only those collections in which closing nets were used (*Smith* 94, 132, 144, 153, 178, and 31), a mean number of 26.8 copepods per cubic meter was calculated for depths between approximately 50 and 150 meters in the eastern Pacific Ocean. Brodsky's data included numerical abundances for seven different vertical levels. For the 50 to 100–m. level he gave a figure of 5,040 calanoids per cubic meter and for the 100 to 200–m. level, 320 per cubic meter. Nine species were present at the former level and ten at the latter level. In comparison, there were no less than 25 species in any of the aforementioned eastern Pacific closing net samples.

TAXONOMY

For each species I have given references to its occurrence in the Pacific Ocean, with the exception of those early records summarized by Giesbrecht and Schmeil (1898) and those cited by Vervoort (1946, 1957). The former reference has usually been omitted in the following sections. I have given measurements for several individuals of a species and usually at all stations where it occurred. The total-length measurements are from the tip of the forehead to the end of the furca, without regard to the telescoped portions of the abdominal segments, and are recorded in mm. unless otherwise indicated. Except for *Pseudochirella*, copepodids which could not be assigned to a species are not mentioned.

Included under Remarks are certain taxonomic or ecological notes and usually a few brief statements on the diagnostic characters of the species. It is hoped that the specific characters mentioned and the figures presented for each species will be useful to others making identifications of tropical calanoid copepods. All illustrations were made with a camera lucida.

Family CALANIDAE

Calanus tenuicornis Dana, 1849

Pacific records: Vervoort, 1946. Also, Yamada, 1933; Johnson, 1942; Mori, 1942; Davis, 1949; Brodsky, 1950; Motoda, Iizuka, and Anraku, 1950; Motoda and Anraku, 1951; Anraku, 1952; Honjo, 1952; Motoda and Anraku, 1952b; Nakai, 1952; Anraku, 1953; Tanaka, 1953; Yamazi, 1953a; 1953c; Anraku, 1954a; 1954b; Motoda and Anraku, 1954; Tsuruta and Chiba, 1954a; 1954b; Yamazi, 1954b; 1954d; Bowman, 1955; Chiba, Tsuruta, and Maéda, 1955; Motoda and Anraku, 1955; Nagaya et al., 1955; Yamazi, 1955a; Chiba, 1956; Tanaka, 1956a; Heinrich, 1957a; Honjo et al., 1957; Heinrich, 1958b; Yamazi, 1958a; 1958b; Brodsky, 1959; Lindberg, 1959; Ponomareva, 1959.

Vessel:	Station	Occurrence
Hugh M. Smith	94	1 female, 1.87 mm.; 1 male, 1.80 mm.
Do	132	present.
Do	153	1 female, 1.75 mm.; 1 male, 1.56 mm.
Do	178	present.
Horizon	32	1 female, 1.68 mm.

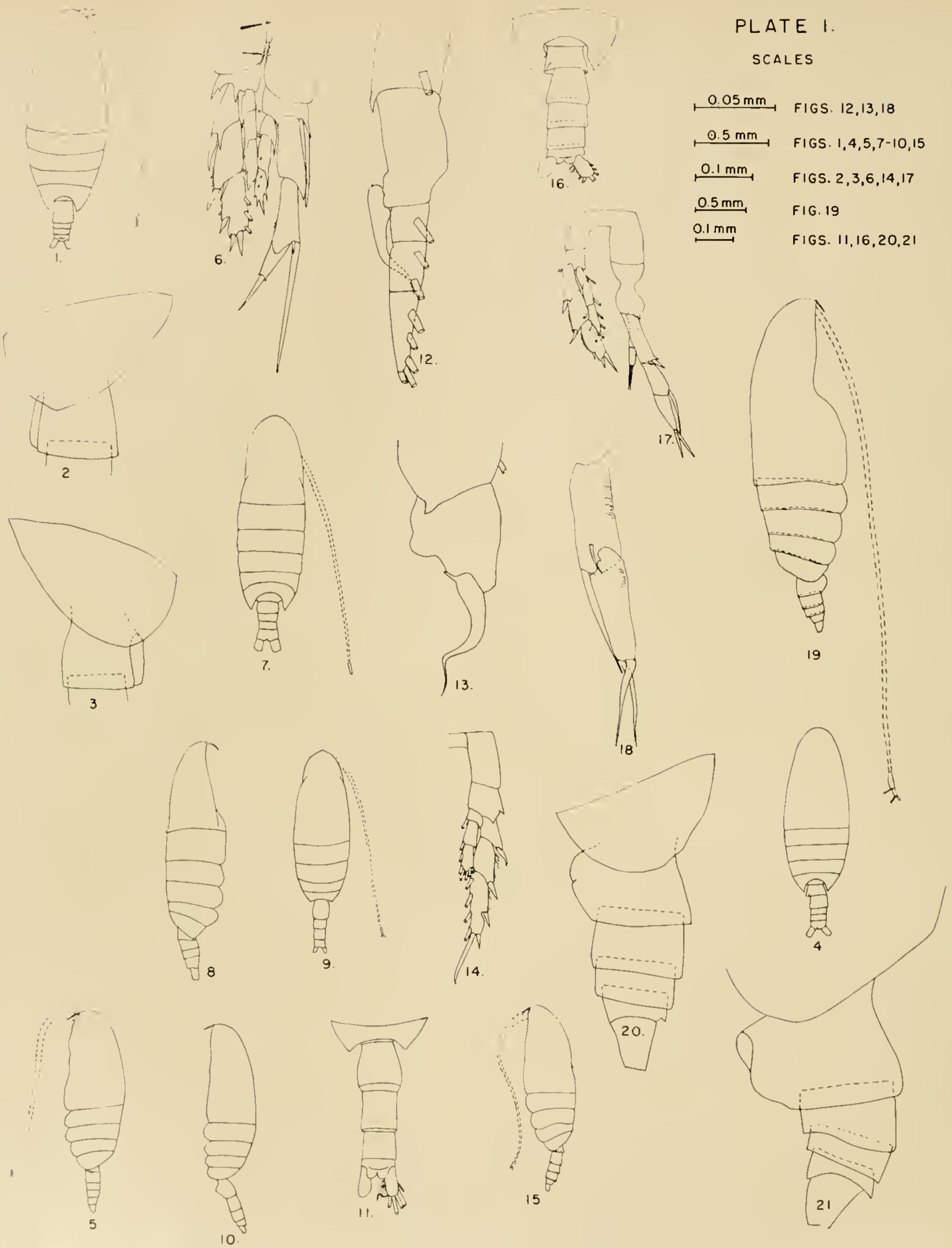

PLATE 1—(1) *Nannocalanus minor*, female, dorsal view; (2) posterior part of thorax and genital segment, left side; (3) posterior part of thorax and genital segment, right side; (4) male, dorsal view; (5) lateral view; (6) fifth pair of feet; (7) stage V female, dorsal view; (8) lateral view; (9) *Canthocalanus pauper*, female, dorsal view; (10) lateral view; (11) posterior part of thorax and abdomen, dorsal view; (12) endopod of first foot, lateral view; (13) first and second basipodal segments of first foot, oblique view; (14) fifth foot; (15) male, lateral view; (16) posterior part of thorax and abdomen, dorsal view; (17) fifth pair of feet; (18) distal two segments of left fifth foot; (19) *Neocalanus gracilis*, female, lateral view; (20) posterior part of thorax and abdomen, lateral view; (21) *Neocalanus robustior*, female, posterior part of thorax and abdomen, lateral view.

Remarks: Most of the present specimens have their furcal setae eroded. Bowman (1955) has previously observed this in specimens collected from the northeastern Pacific. He attributed this erosion to protozoan parasites which were present in the furcae. The majority of my specimens also contain these parasites in the furcae. Bowman (1955) has fully figured *C. lighti*, a species which differs morphologically from *tenuicornis* only in size.

Nannocalanus minor (Claus, 1863)

(Plate 1, figs. 1–8)

Pacific records: Vervoort, 1946. Also, as *Calanus minor;* Yamada, 1933a; Mori, 1937; 1942; Wilson, 1942; Anraku, 1952; Chiba, 1952c; Honjo, 1952; Nakai, 1952; Tanaka, 1953; Yamazi, 1953a; 1953b; 1953c; Anraku, 1954b; Motoda and Anraku, 1954; Tsuruta and Chiba, 1954b; Yamazi, 1954b; 1954d; Chiba, Tsuruta, and Maéda, 1955; Hida and King, 1955; Motoda and Anraku, 1955; Nagaya et al., 1955; Yamazi, 1955d; Chiba, 1956; Tanaka, 1956a; Honjo et al., 1957; Yamazi, 1958a. As *Nannocalanus minor;* Wilson, 1950; Brodsky, 1955; Rose, 1955; Heinrich, 1957b; 1958a; Brodsky, 1959.

Vessel:	*Station*	*Occurrence*
Hugh M. Smith	94	1 female, 1.73 mm.
Do	132	14 females, 1.56–1.70 mm.; 7 males, 1.39–1.43 mm.
Do	144	1 female, 1.73 mm.
Do	153	10 females, 1.58–1.67 mm.; 3 males, 1.44–1.46 mm.
Do	178	25 females, 1.51–1.65 mm.; 12 males, 1.31–1.51 mm.
Do	31	1 female, 1.75 mm.
Do	29	1 female, 1.80 mm.
Do	63	1 female, 1.80 mm.
Stranger	34	6 females, 1.53–1.70 mm.
Orsom	10	2 females, 1.58, 1.61 mm.; 4 males 1.24–1.46 mm.
Horizon	32	9 females (stage V), 1.53–1.70 mm.

Remarks: All the above female specimens belong to *N. minor* f. *major* (Sewell, 1929). Although Sewell (1947) has recently recognized two forms of the male (f. *major* and f. *minor*), I was unable to distinguish these forms among the above specimens. Presumably, they are all referable to f. *major* as Vervoort (1946) has reported smaller males (1.20–1.29) from one *Snellius* station (113) in Netherlands East Indies.

Canthocalanus pauper (Giesbrecht, 1888)

(Plate 1, figs. 9–18)

Pacific records: Vervoort, 1946. Also, as *Calanus pauper;* Mori, 1937; 1942; Honjo, 1952; Yamazi, 1953a; 1953b; Anraku, 1954b; Johnson, 1954; Tsuruta and Chiba, 1954b; Motoda and Anraku, 1955; Nagaya et al., 1955. As *Canthocalanus pauper;* Wilson, 1942; 1950; Tanaka, 1953; Brodsky, 1955; Rose, 1955; Tanaka, 1956a; Yamazi, 1958a.

Vessel:	*Station*	*Occurrence*
Hugh M. Smith	63	1 female, 1.42 mm.
Stranger	34	1 male, 1.31 mm.
Orson	32	2 females, 1.42, 1.46 mm.; 1 male, 1.36 mm.

Remarks: This small copepod is most easily recognized by the peculiarly shaped spine on the second basipodal segment of the first pair of feet (figs. 12, 13) in the female and the structure of the fifth pair of feet (figs. 17, 18) in the male.

Neocalanus gracilis (Dana, 1849)

(Plate 1, figs. 19–20)

Pacific records: Vervoort, 1946; 1957. Also, as *Calanus gracilis;* Mori, 1942; Honjo, 1952; Tsuruta and Chiba, 1954b; Motoda and Anraku, 1955; Nagaya et al., 1955; Chiba, 1956; Honjo et al., 1957. As *Neocalanus gracilis;* Tanaka, 1953; Hida and King, 1955; Tanaka, 1956a; Yamazi, 1958a.

Vessel:	*Station*	*Occurrence*
Hugh M. Smith	94	present.
Do	132	8 females (stage V), 2.34–2.48 mm.
Do	153	1 female, 3.09 mm.
Do	31	2 females, 3.33 mm.
Stranger	34	4 females, 3.01–3.06 mm.
Orsom	10	1 female, 2.96 mm.
Satsuma	32	1 female, 2.11 mm.

Remarks: Vervoort (1946) has listed the differences between this species and *Neocalanus robustior* (Giesbrecht). The adult females of *N. gracilis* are smaller (maximum 3.33) and the genital segment is less produced ventrally (fig. 20). No males were encountered in the present collections.

Neocalanus robustior (Giesbrecht, 1888)

(PLATE 1, FIG. 21)

Pacific records: Vervoort, 1946. Also, as *Calanus robustior;* Mori, 1937; Honjo, 1952; Yamazi, 1953a; Tsuruta and Chiba, 1954b; Chiba, Tsuruta, and Maéda, 1955; Nagaya et al., 1955; Chiba 1956; Honjo et al., 1957. As *Neocalanus robustior;* Wilson, 1942; 1950; Tanaka, 1953; Brodsky, 1955; Tanaka, 1956a; Yamazi, 1958a.

Vessel:	*Station*	*Occurrence*
Hugh M. Smith	153	1 female, 4.08 mm.
Do	178	1 female, 3.40 mm.
Do	63	1 female (stage V), 2.99 mm., 3 females, 3.80–3.89 mm.
Stranger	34	1 female, 3.61 mm.

Remarks: The large size (greater than 3.4 mm.) and greatly produced genital segment (fig. 21) of this species distinguishes it from *N. gracilis*. No males were found in the present samples.

Undinula vulgaris (Dana, 1849)

Pacific records: Vervoort, 1946. Also, as *Calanus vulgaris;* Yamada, 1933a; Mori, 1937; 1942; Chiba, 1952c; Honjo, 1952; Anraku, 1954b; Tsuruta and Chiba, 1954b; Motoda and Anraku, 1955; Chiba, 1956; Honjo et al., 1957. As *Undinula vulgaris;* Wilson, 1942; Johnson, 1949; Wilson, 1950; Tanaka, 1953; Johnson, 1954; Brodsky, 1955; Hida and King, 1955; Rose, 1955; Tanaka, 1956a; Yamazi, 1958a.

Vessel:	*Station*	*Occurrence*
Satsuma	32	1 male, 2.04 mm.

Remarks: Both Vervoort (1946) and Wilson (1950) speak of the great abundance of this species in the Netherlands East Indies and near the Hawaiian Islands, respectively. Scott (1909) also found it abundantly in the Malay Archipelago area as did Johnson (1949) in Bikini Lagoon and Tanaka (1956a) in the Izu region of Japan. In view of its extreme scarcity in the present collections, it is apparently more of an insular and nearshore species in contradistinction to *Undinula darwini*, a widespread species in the present collections.

Undinula darwini (Lubbock, 1860)

(PLATE 2, FIGS. 1–9)

Pacific records: Vervoort, 1946. Also, as *Calanus darwini;* Yamada, 1933a; Mori, 1937; 1942; Anraku, 1952; Honjo, 1952; Nakai, 1952; Yamazi, 1953a; 1953b; 1953c; Anraku, 1954b; Chiba and Tsuruta, 1954; Yamazi, 1954b; Motoda and Anraku, 1955; Nagaya et al., 1955; Yamazi, 1955a; 1955d; Chiba, 1956; Honjo et al., 1957; Yamazi, 1958b. As *Undinula darwini;* Wilson, 1942; 1950; Tanaka, 1953; Johnson, 1954; Brodsky, 1955; Rose, 1955; Tanaka, 1956a; Heinrich, 1957b; 1958a; Yamazi, 1958a; 1958b.

Remarks: All female specimens of this species have a group of inwardly projecting spines on the inner sides of the fifth thoracic segment (fig. 1). Also characteristic of this sex is the shape of the genital segment, which in dorsal view, is seen to narrow anteriorly (fig. 1).

The three forms of the female of this species (described by Sewell, 1929) are distinguished by the shape of the left fifth thoracic margin and spinulation of the proximal segments of the first antennae. The right fifth thoracic margin in all three forms is rounded and has

Vessel:	*Station*	*Occurrence (measurement in mm.; number of specimens in paren.)* f. *typica* female	f. *symmetrica* female	f. *intermedia* female	male
Hugh M. Smith	94				(1)
Do	132		1.97 (1)		
Do	144	1.90 (1)	1.87–2.04 (7)		1.80 (3)
Do	153	1.90–2.00 (2)	1.80–1.90 (7)		present.
Do	178	present	1.84–1.90 (20)		1.60–1.67 (4)
Do	30	2.00 (2)	1.95–2.04 (4)		
Do	31	1.90–2.18 (2)	2.00 (1)		(2)
Do	29				(1)
Do	63	1.90 (1)	1.94–2.04 (5)		(8)
Stranger	34	2.04 (1)	2.04 (1)	2.07 (1)	(3)
Orsom	10			1.90 (1)	1.73 (1)
Horizon	32		2.04 (1)	1.94–2.07 (4)	
Satsuma	32	1.80 (1)		1.84–1.90 (5)	1.63 (1)

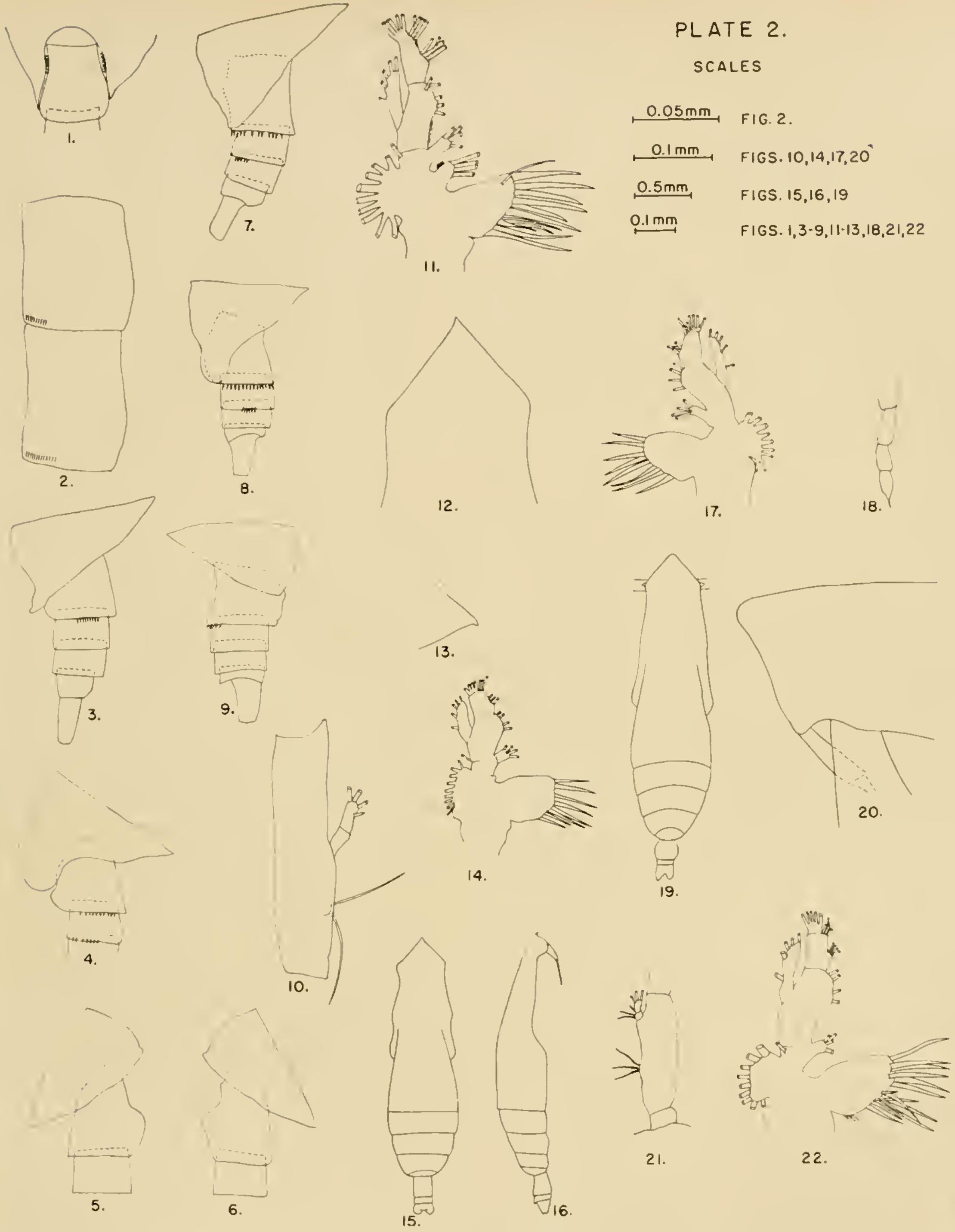

Plate 2.—(1) *Undinula darwini* f. *typica*, female, posterior part of thorax and genital segment, dorsal view; (2) segments 6 and 7 of first antenna; (3) posterior part of thorax and abdomen, left side; (4) posterior part of thorax and abdomen, left side; (5) *U. darwini* f. *symmetrica*, female, posterior part of thorax and genital segment, right side; (6) posterior part of thorax and genital segment, left side; (7) *U. darwini* f. *intermedia*, female, posterior part of thorax and abdomen, left side; (8) posterior part of thorax and abdomen, left side; (9) posterior part of thorax and abdomen, right side; (10) *Eucalanus attenuatus*, female, second basal segment and endopod of mandible; (11) first maxilla; (12) *E. mucronatus*, stage IV, female, forehead, dorsal view; (13) forehead, lateral view; (14) first maxilla; (15) stage V, male, dorsal view; (16) lateral view; (17) first maxilla; (18) fifth foot; (19) *E. subtenuis* var. *japonica*, female, dorsal view; (20) forehead, lateral view; (21) basal segments and endopod of mandible; (22) first maxilla.

a small notch. In forma *typica,* both segments 6 and 7 of the first antennae have a row of spinules along the distal margin (fig. 2). The left fifth thoracic margin is somewhat variable in shape. Typically, it is produced into a point which is directed ventrally (fig. 3). In a few individuals this margin was expanded and rounded (fig. 4). In forma *symmetrica,* a row of spinules is also present on segments 6 and 7 of the first antennae, but the two thoracic margins are symmetrical (figs. 5, 6). In forma *intermedia,* spinules are present on segments 3 through 7 of the first antennae, and the left fifth thoracic margin is usually more or less triangular in shape (fig. 7). In several specimens, this margin was rounded similar to that of forma *symmetrica* (fig. 8). Most examples of forma *intermedia* also had a small group of spines situated on the left mid-lateral margin of the second abdominal segment.

Chiba (1953a) has recently discussed and presented figures of small (40–60μ) spherical bodies which he detected within the furcae of the female of this species. He considered these objects to be eggs and analogized the "egg chamber" (furca) to the brood sac of daphnids. I too have seen these bodies in the furcae of this species. They are possibly protozoan parasites but not the reproductive eggs of the species.

Family EUCALANIDAE

Eucalanus attenuatus (Dana, 1849)

(PLATE 2, FIGS. 10, 11)

Pacific records: Vervoort, 1946. Also, Yamada, 1933a; Tanaka, 1935a; Mori, 1937; Johnson, 1942; Mori, 1942; Wilson, 1942; Brodsky, 1950; Wilson, 1950; Anraku, 1952; Honjo, 1952; Tanaka, 1953; Yamazi, 1953c; Anraku, 1954b; Johnson, 1954; Tsuruta and Chiba, 1954b; Yamazi, 1954d; Brodsky, 1955; Chiba, Tsuruta and Maéda, 1955; Hida and King, 1955; Motoda and Anraku, 1955; Nagaya et al., 1955; Rose, 1955; Yamazi, 1955a; 1955d; Chiba, 1956; Tanaka, 1956a; Honjo et al., 1957; Heinrich, 1958a; 1958b; Yamazi, 1958a; Brodsky, 1959; Lindberg, 1959; Ponomareva, 1959.

Vessel:	*Station*	*Occurrence*
Hugh M. Smith	132	1 female, 3.89 mm.
Do	153	present.
Do	178	2 females, 3.61, 3.80 mm.; 1 male, 2.96 mm.
Do	30	1 female, 3.16 mm.
Do	31	5 males, 2.92–3.06 mm.
Do	63	2 females, 3.90, 4.08 mm.
Stranger	34	1 female, 3.06 mm.
Horizon	32	7 females, 3.90–4.28 mm.; 1 female (stage V) 3.20 mm.

Remarks: Vervoort (1946) noted that there were large variations in the sizes of his specimens (females, 3.55–5.80; males 2.95–4.35) from the Netherlands East Indies, but he could find no anatomical differences between the size groups. Tanaka (1956a) likewise observed that there were large size variations (female, 4.32–6.19; male, 3.24–4.67) in the lengths of specimens obtained from the Izu region of Japan. He reported differences (shape of genital segment, presence of hair on female, relative lengths of segments of fifth pair of feet in the male) between the larger specimens of this species and suggested that a northern variety may have been present. The lengths of the present specimens were not nearly so variable as those reported by Vervoort or Tanaka.

Eucalanus mucronatus Giesbrecht, 1888

(PLATE 2, FIGS. 12–18)

Pacific records: Vervoort, 1946; 1957. Also, Yamada, 1933; Tanaka, 1935a; Honjo, 1952; Nakai, 1952; Tanaka, 1953; Yamazi, 1953a; Anraku, 1954b; Chiba, Tsuruta, and Maéda, 1955; Motoda and Anraku, 1955; Nagaya et al., 1955; Tanaka, 1956a; Honjo et al., 1957; Yamazi, 1958a; 1958b.

Vessel:	*Station*	*Occurrence*
Horizon	32	1 female (stage IV), 2.07 mm.; 1 male (stage V), 2.55 mm.

Remarks: Juveniles of this species were found in one collection. They are easily recognized by the pointed forehead, which is present in both sexes.

Eucalanus subtenuis Giesbrecht, 1888

(PLATE 2, FIGS. 19–21; PLATE 3, FIGS. 1–4)

Pacific records: Vervoort, 1946. Also, Mori, 1937; Tanaka, 1935a; Johnson, 1942; Mori, 1942; Wilson, 1942; 1950; Tanaka, 1953; 1956a; Fukase, 1957; Honjo et al., 1957; Heinrich, 1958b.

Vessel:	*Station*	*Occurrence*
Hugh M. Smith	94	1 female, 3.12 mm.
Do	132	13 females, 2.55–2.96 mm.
Do	144	10 females, 2.40–2.60 mm.
Do	153	present.
Do	178	15 females, 2.65–2.72 mm.; 6 males, 2.45–2.52 mm.
Do	31	15 females, 2.55–2.79 mm.
Do	63	16 females, 2.69–2.96 mm.; 1 male, 2.51 mm.

Remarks: All of the present specimens are referable to *E. subtenuis* var. *japonica* Fukase, 1957. This variety is distinguished from *subtenuis* chiefly by the number of setae on the mandibular palpus (both sexes) and the structure of the fifth feet of the male. There are 3 setae on the mandibular palpus (fig. 21; fig. 3) and the distal segment of the fifth foot is longer than the terminal spine (fig. 4). In *subtenuis* there are 2 setae on the mandibular palpus and the terminal spine of the fifth foot is longer than the distal segment.

According to Fukase, Tanaka's (1935a) *E. subtenuis* and Mori's (1937) *E. mucronatus* are both referable to *subtenuis* var. *japonica.*

This species was present in seven of the samples and in four of these (*Smith* 132, 144, 178, 63) it was the most abundant species.

Eucalanus pileatus Giesbrecht, 1888

(PLATE 3, FIGS. 5–12)

Pacific records: Scott, 1909; Tanaka, 1935a; Wilson, 1950; Tanaka, 1953; 1956a.

Vessel:	*Station*	*Occurrence*
Satsuma	32	2 females, 1.80 and 1.94 mm.

Remarks: This species closely resembles *E. subcrassus* and the two may prove to be conspecific. Until a detailed study is made of each, it seems best to keep them separate. The females may be distinguished as follows (Pacific specimens):

1. Size. *E. pileatus*, 1.80–2.41; *E. subcrassus*, 2.23–2.82. (length data from Tanaka, 1935a; Mori, 1937; Vervoort, 1946; and present data). Farran (1936) has reported *E. subcrassus* with total lengths of 1.84–2.92 from the Great Barrier Reef. He did not record *E. pileatus.*
2. Shape of forehead. In dorsal view anterior end of forehead more produced in *E. pileatus* (fig. 7) than in *E. subcrassus* (plate 3, fig. 15).
3. Shape of genital segment. *E. pileatus*, greatest diameter at a point approximately one-half the length of the segment (fig. 10); *E. subcrassus*, greatest diameter in lower third of segment (plate 3, fig. 16).

Eucalanus subcrassus Giesbrecht, 1888

(PLATE 3, FIGS. 13–17)

Pacific records: Vervoort, 1946. Also, Tanaka, 1935a; Mori, 1937; 1942; Wilson, 1950; Anraku, 1952; Honjo, 1952; Tanaka, 1953; Anraku, 1954b; Tsuruta and Chiba, 1954b; Brodsky, 1955; Chiba, Tsuruta, and Maéda, 1955; Motoda and Anraku, 1955; Nagaya et al., 1955; Rose, 1955; Tanaka, 1956a; Honjo et al., 1957; Yamazi, 1958a.

Vessel:	*Station*	*Occurrence*
Hugh M. Smith	63	3 females, 2.44–2.52 mm.
Stranger	34	3 females, 2.24–2.48 mm.
Orsom	10	4 females, 2.31–2.48 mm., 3 males (stage V), 2.11–2.18 mm.

Remarks: Vervoort (1946) stated that there are 4 setae on the second basal joint of the first maxilla. The present specimens, however, have 5 (fig. 17).

Rhincalanus cornutus (Dana, 1849)

(PLATE 3, FIGS. 18–19)

Pacific records: Vervoort, 1946. Also, Yamada, 1933; Tanaka, 1935a; Mori, 1937; 1942; Wilson, 1942; 1950; Honjo, 1952; Tanaka, 1953; Anraku, 1954b; Tsuruta and Chiba, 1954b; Chiba, Tsuruta and Maéda, 1955; Hida and King, 1955; Nagaya et al., 1955; Rose, 1955;

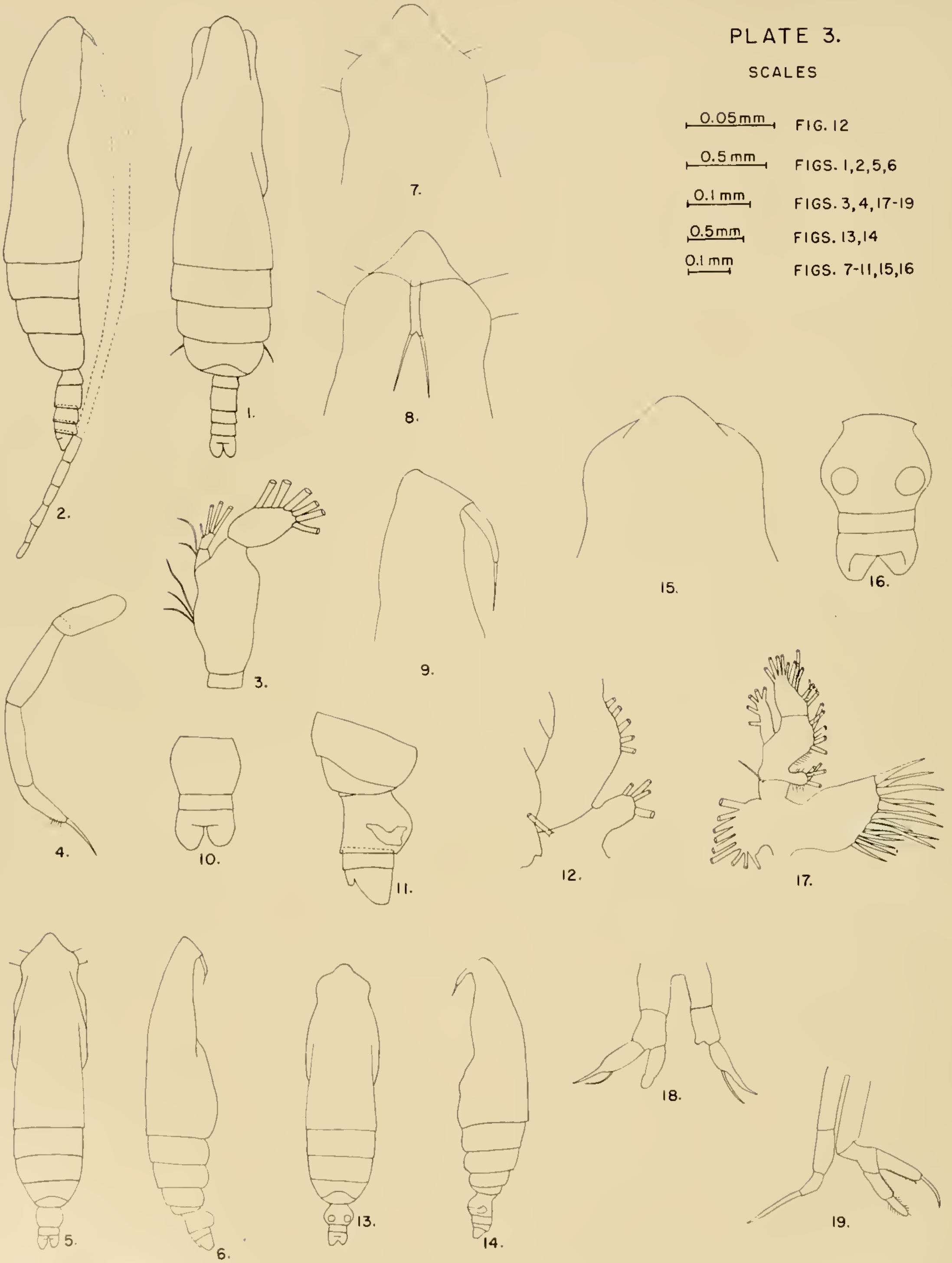

PLATE 3.—(1) *Eucalanus subtenuis* var. *japonica*, male, dorsal; (2) lateral; (3) mandible palpus; (4) fifth foot; (5) *E. pileatus*, female, dorsal view; (6) female, lateral view; (7) forehead, dorsal view; (8) forehead, ventral view; (9) forehead, lateral view; (10) abdomen, dorsal view; (11) posterior part of thorax and abdomen, lateral view; (12) first maxilla (part); (13) *E. subcrassus*, female, dorsal view; (14) lateral view; (15) forehead, dorsal view; (16) abdomen, dorsal view; (17) first maxilla; (18) *Rhincalanus cornutus*, stage V, male, fifth pair of feet; (19) adult male, fifth pair of feet.

Chiba, 1956; Tanaka, 1956a; Honjo et al., 1957; Yamazi, 1958a.

Vessel:	*Station*	*Occurrence*
Hugh M. Smith	94	2 females, 2.79, 3.20 mm.
Do	144	1 female, 3.09 mm.
Do	153	1 male, 2.89 mm.
Do	31	2 females, 3.33; 2 males (stage V), 2.70, 2.80 mm.
Do	29	18 females, 3.20–3.33 mm.; 6 males, 2.79–2.86 mm.
Do	63	3 females, 3.09–3.24 mm.
Stranger	34	1 female, 3.09 mm.
Orsom	10	2 males, 2.69, 2.72 mm.
Horizon	32	2 females, 3.40 mm.; 1 male (stage V), 2.52 mm.
Satsuma	32	1 male, 2.95 mm.

Remarks: All of the above females belong to *R. cornutus* f. *typica* Schmaus. This species was widely distributed in the samples.

Rhincalanus nasutus Giesbrecht, 1888

Pacific records: Vervoort, 1946; 1957. Also, Yamada, 1933; Tanaka, 1935a; Johnson, 1942; Brodsky, 1950; Anraku, 1952; Honjo, 1952; Tanaka, 1953; Anraku, 1954b; 1954c; Chiba and Tsuruta, 1955; Tanaka, 1956a; Honjo et al., 1957; Heinrich, 1958a; Yamazi, 1958a.

Vessel:	*Station*	*Occurrence*
Hugh M. Smith	94	4 females, 4.08–4.37 mm.

Remarks: This species occurred in but one sample which was collected in the eastern Pacific by a closing net at a depth between 146 and 172 meters. As Vervoort (1946) mentioned, it is primarily a subsurface species.

Family PARACALANIDAE

Paracalanus aculeatus Giesbrecht, 1888

(Plate 4, figs. 1–3)

Pacific records: Vervoort, 1946; 1957. Also, Yamada, 1933a; 1933b; Mori, 1942; Anraku, 1952; Chiba, 1952a; 1952b; Honjo, 1952; Nakai, 1952; Anraku, 1953; Tanaka, 1953; Yamazi, 1953c; Anraku, 1954b; Tsuruta and Chiba, 1954b; Chiba, Tsuruta, and Maéda, 1955; Motoda and Anraku, 1955; Nagaya et al., 1955; Rose, 1955; Chiba, 1956; Tanaka, 1956b; Honjo et al., 1957; Yamazi, 1958a.

Vessel:	*Station*	*Occurrence*
Hugh M. Smith	144	1 female, 1.0 mm.
Do	153	2 females, 1.09, 1.17 mm.
Do	178	2 females, 1.10 mm.
Do	31	1 female, 1.10 mm.
Do	63	9 females, 1.04–1.16 mm.
Stranger	34	4 females, 1.07–1.17 mm.
Orsom	10	3 females, 1.07–1.12 mm.
Horizon	32	2 females, 1.05, 1.10 mm.

Remarks: All the present specimens belong to *P. aculeatus* f. *major* Sewell, 1929. It was widely distributed in the present collections, but no males were observed.

Paracalanus parvus (Claus, 1863)

Pacific records: Vervoort, 1946; 1957. Also, Mori, 1942; Lowe, 1936; Chiba, 1949; Kokubo, 1950; Yamazi, 1950; 1951; Anraku, 1952; Honjo, 1952; Motoda and Anraku, 1952a; Yamazi, 1952a; 1952b; 1952c; Anraku, 1953; Tanaka, 1953; Yamazi, 1953a; 1953b; 1953c; Anraku, 1954a; 1954b; Tsuruta and Chiba, 1954b; Yamazi, 1954a; 1954b; 1954c; 1954d; 1954e; Chiba, Tsuruta, and Maéda, 1955; Motoda and Anraku, 1955; Nagaya et al., 1955; Nakai, 1955; Rose, 1955; Yamazi, 1955a; 1955b; 1955c; 1955d; Chiba, 1956; Shen and Bai, 1956; Tanaka, 1956b; Honjo et al., 1957; Légaré, 1957; Yamazi, 1957; 1958a; 1958b; Brodsky, 1959; Lindberg, 1959.

Vessel:	*Station*	*Occurrence*
Hugh M. Smith	94	2 females, 0.99 mm.

Remarks: Although this is a cosmopolitan species, it was observed in but one sample. Possibly its small size permitted most of the specimens to pass through the meshes of the nets employed or perhaps it is not too abundant in the waters sampled.

Paracalanus dubia Sewell, 1912

(Plate 4, figs. 4–12)

Pacific records: Rose, 1955.

Vessel:	*Station*	*Occurrence*
Kagoshima	613	1 female, 0.49 mm.

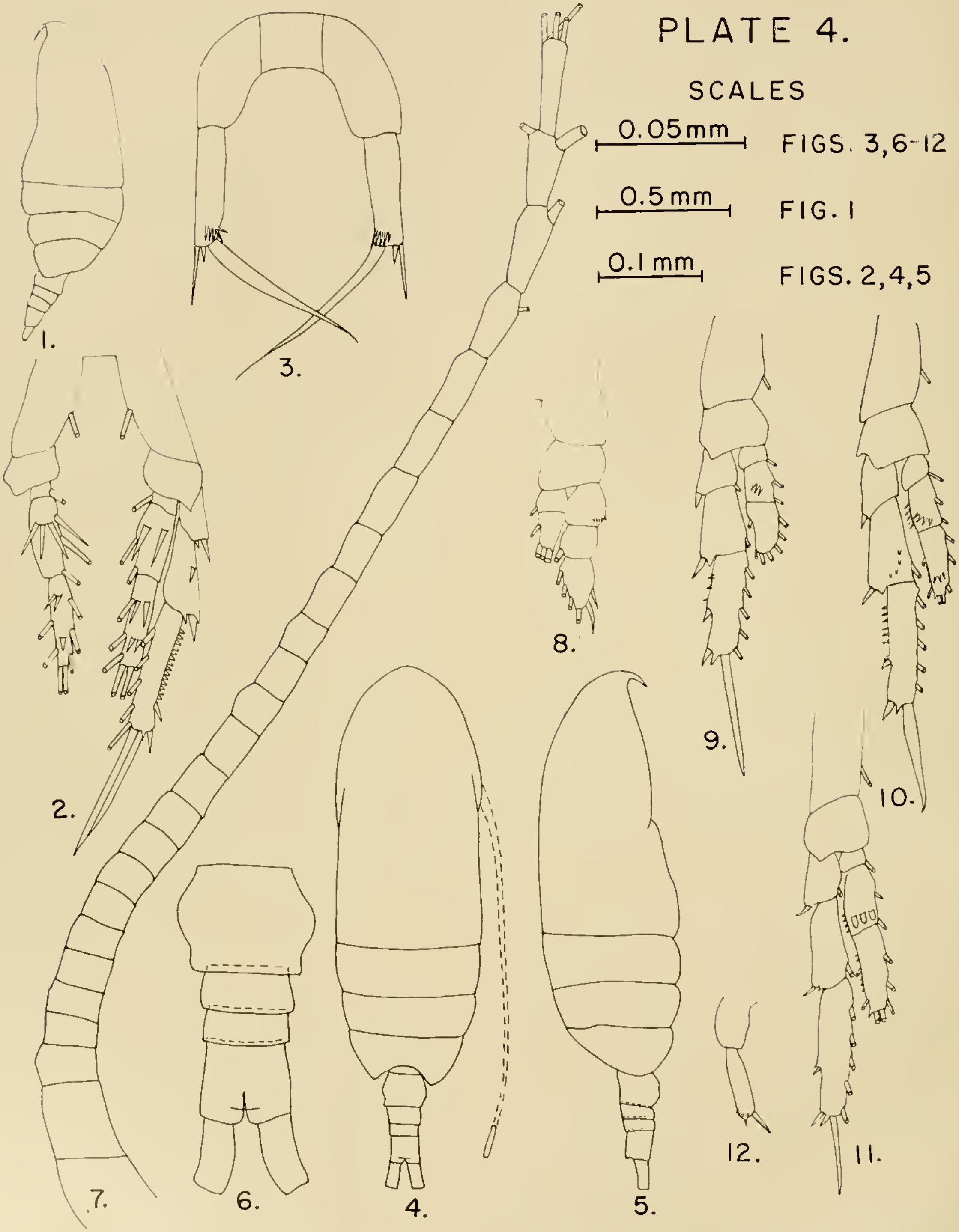

PLATE 4.—(1) *Paracalanus aculeatus*, female, lateral view; (2) fourth pair of feet (one exopod missing); (3) fifth pair of feet; (4) *P. dubia*, female, dorsal view; (5) lateral view; (6) abdomen, dorsal view; (7) first antenna; (8) first foot; (9) second foot; (10) third foot; (11) fourth foot; (12) fifth foot.

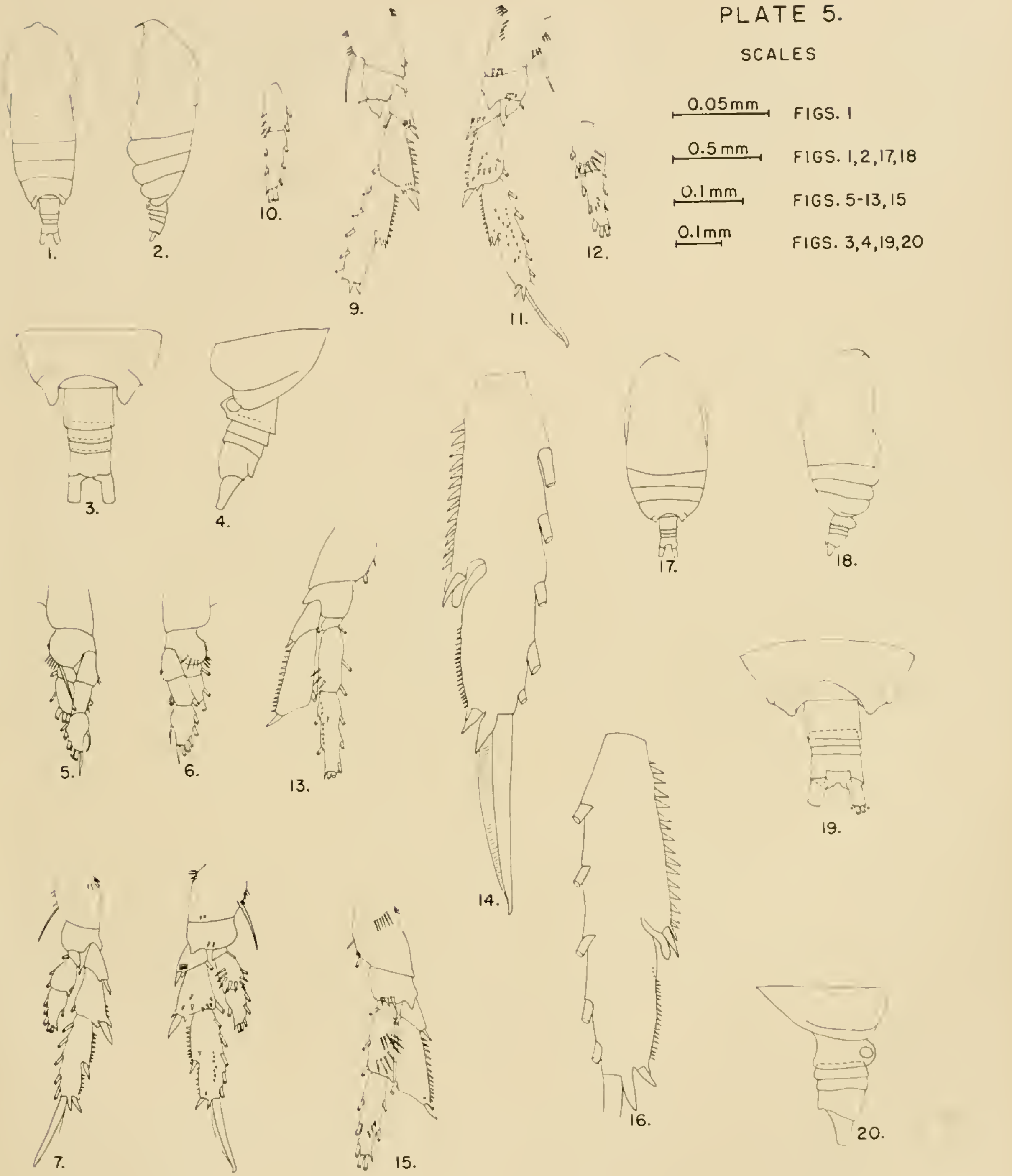

Plate 5.—(1) *Acrocalanus longicornis*, female, dorsal view; (2) lateral view; (3) posterior part of thorax and abdomen, dorsal view; (4) posterior part of thorax and abdomen, lateral view; (5) first foot, anterior; (6) first foot, posterior; (7) second foot, anterior; (8) second foot, posterior; (9) third foot, anterior, without distal 2 segments of endopod; (10) distal 2 segments of endopod of third foot, anterior; (11) third foot, posterior, without distal 2 segments of endopod; (12) distal 2 segments of endopod, posterior; (13) fourth foot, anterior, without third exopodal segment; (14) third exopodal segment of fourth foot, anterior; (15) fourth foot, posterior, without third exopodal segment; (16) third exopodal segment of fourth foot, posterior; (17) *A. andersoni*, female, dorsal view; (18) lateral view; (19) posterior part of thorax and abdomen, dorsal view; (20) posterior part of thorax and abdomen, lateral view.

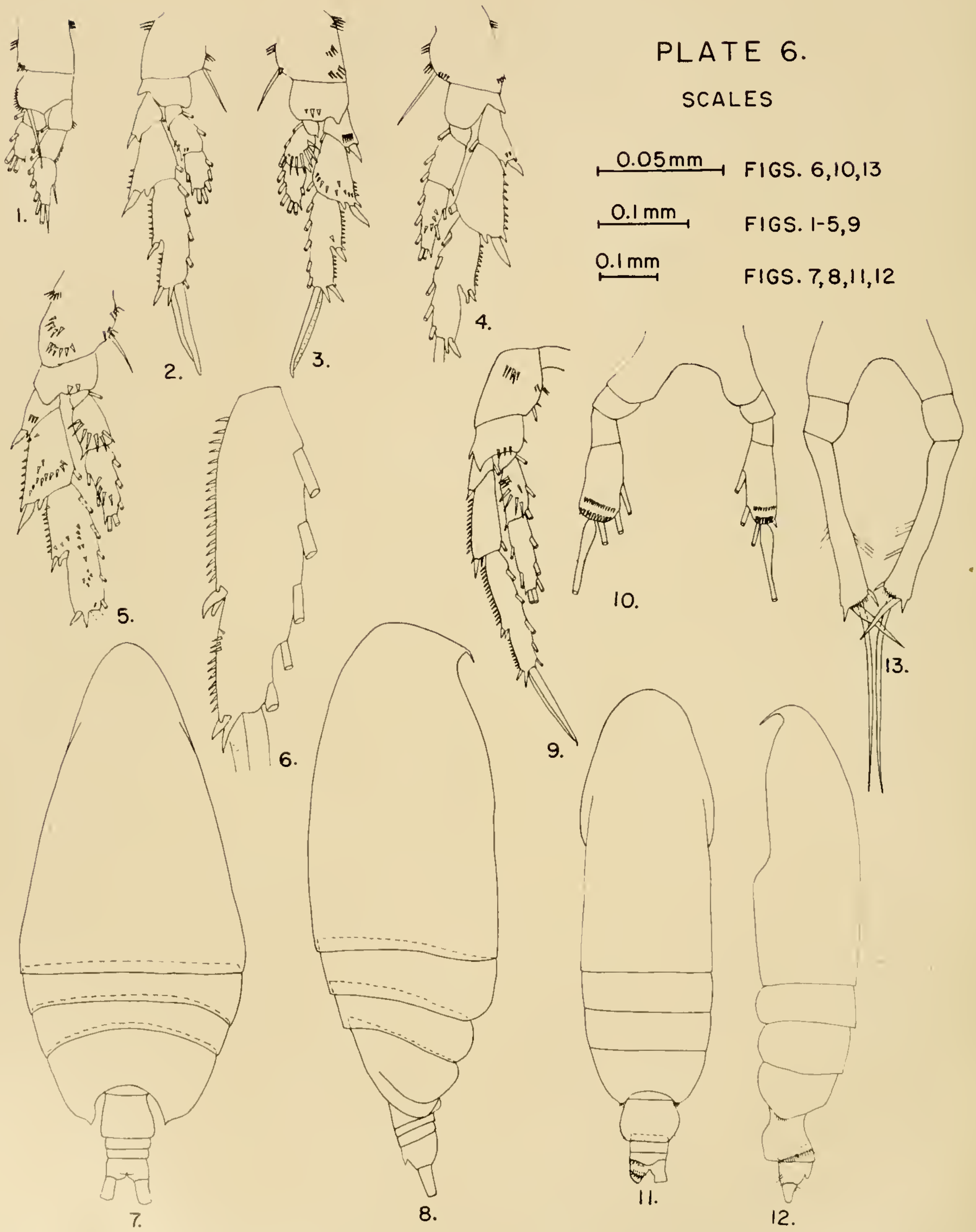

Plate 6.—(1) *Acrocalanus andersoni,* first foot, anterior; (2) second foot, anterior; (3) second foot, posterior; (4) third foot, anterior; (5) third foot, posterior; (6) third exopodal segment of fourth foot, posterior; (7) *A. monachus,* female, dorsal view; (8) lateral view; (9) fourth foot, posterior; (10) *Calocalanus pavo,* female, fifth pair of feet; (11) *C. plumulosus,* female, dorsal view; (12) lateral view; (13) fifth pair of feet.

Remarks: The forehead of the present specimen as well as the spination of certain of the first four pairs of swimming feet differ somewhat from Sewell's description. The fifth pair of feet of Sewell's *P. serratipes* are similar to those of *P. dubia* but the former is a larger species (1.10 mm.).

The small spinules on the distal end of the terminal segment of the fifth feet can best be seen under oil immersion. The other feet, except the first pair, were also examined under oil in order to ascertain the number of setae, surface spines and lateral teeth on the various segments.

Only one specimen was obtained and this was partly destroyed in the process of dissection.

Acrocalanus longicornis Giesbrecht, 1888

(Plate 5, figs. 1–16)

Pacific records: Vervoort, 1946. Also, Yamada, 1933; Mori, 1937; 1942; Wilson, 1942; 1950; Tanaka, 1953; Tsuruta and Chiba, 1954b; Chiba, Tsuruta and Maéda, 1955; Nagaya et al., 1955; Rose, 1955; Yamazi, 1955a; Tanaka, 1956b; Honjo et al., 1957; Yamazi, 1958a.

Vessel:	*Station*	*Occurrence*
Hugh M. Smith	153	2 females, 1.20, 1.22 mm.
Do	31	1 female, 1.26 mm.
Do	63	2 females, 1.19, 1.24 mm.
Stranger	34	7 females, 1.17–1.27 mm.

Remarks: The presence of a partial suture between the head and first thoracic segment (figs. 1, 2) and the spination of the swimming feet, particularly the number of teeth (more than 18) on the distal part of the third exopodal segment of the fourth pair of feet (figs. 14, 16), distinguished this species from others in the genus.

Acrocalanus andersoni Bowman, 1958

(Plate 5, figs. 17–20; Plate 6, figs. 1–6)

Pacific records: None.

Vessel:	*Station*	*Occurrence*
Stranger	34	1 female, 0.95 mm.
Orsom	10	3 females, 1.12–1.17 mm.
Kagoshima	613	1 female, 1.12 mm.

Remarks: This species was recently described from specimens obtained from the south Atlantic coast of the United States (Bowman, 1958). It is recognized by the lack of partial suture between the head and first thoracic segment (figs. 17, 18) and the number of lateral teeth (11) on the distal part of the third exopodal segment of the fourth pair of feet (fig. 6).

Acrocalanus monachus Giesbrecht, 1888

(Plate 6, figs. 7–9)

Pacific records: Scott, 1909; Farran, 1936; Mori, 1937; 1942; Wilson, 1942; 1950; Tanaka, 1953; Tsuruta and Chiba, 1954b; Chiba, Tsuruta, and Maéda, 1955.

Vessel:	*Station*	*Occurrence*
Stranger	34	2 females, 1.02, 1.05 mm.
Orsom	10	1 female, 1.00 mm.
Horizon	32	3 females, 1.00–1.10 mm.

Remarks: The truncate appearance of this species in lateral view (fig. 8) readily distinguishes it from others in the genus.

Calocalanus pavo (Dana, 1849)

(Plate 6, fig. 10)

Pacific records: Vervoort, 1946. Also, Yamada, 1933a; Mori, 1937; Johnson, 1942; Mori, 1942; Wilson, 1942; 1950; Tanaka, 1953; Yamazi, 1953b; 1953c; Johnson, 1954; Tsuruta and Chiba, 1954b; Yamazi, 1954d; Brodsky, 1955; Chiba, Tsuruta, and Maéda, 1955; Nagaya et al., 1955; Rose, 1955; Yamazi, 1955d; Chiba, 1956; Tanaka, 1956b; Heinrich, 1957b; Honjo et al., 1957; Heinrich, 1958b; Yamazi, 1958a; 1958b.

Vessel:	*Station*	*Occurrence*
Hugh M. Smith	153	1 female, 0.85 mm.
Do	63	1 female, 1.00 mm.
Stranger	34	1 female, 1.19 mm.
Orsom	10	1 female, 0.97 mm.
Horizon	32	1 female, 1.00 mm.

Remarks: Bernard (1958) has recently revised the genus *Calocalanus* based on material collected in the Bay of Algiers. She proposed the family Calocalanidae, which consists of the genus *Calocalanus* s. str. and two new genera, *Leptocalanus* and *Dolichocera*. She has also

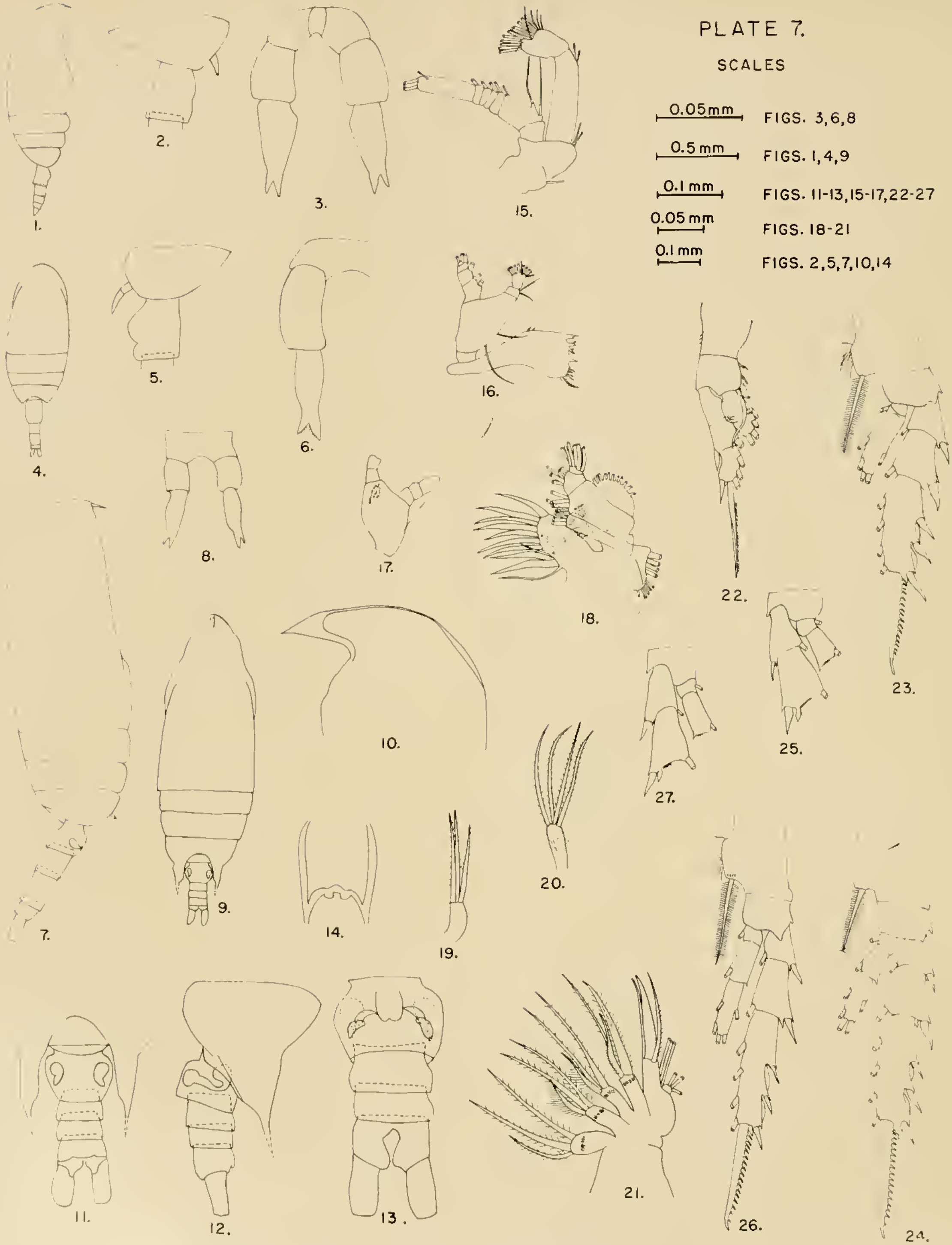

PLATE 7.—(1) *Clausocalanus arcuicornis* f. *major*, female, lateral view; (2) posterior part of thorax and genital segment, lateral view; (3) fifth pair of feet; (4) *C. arcuicornis* f. *minor*, female, dorsal view; (5) posterior part of thorax and genital segment, lateral view; (6) fifth foot; (7) *C. furcatus*, female, lateral view; (8) fifth pair of feet; (9) *Euaetideus giesbrechti*, female, dorsal view; (10) forehead, lateral view; (11) posterior part of thorax and abdomen, dorsal view; (12) posterior part of thorax and abdomen, lateral view; (13) abdomen, ventral view; (14) rostrum; (15) second antenna; (16) mandible; (17) mandible palpus (other side); (18) first maxilla; (19) second inner lobe of first maxilla; (20) third inner lobe of first maxilla; (21) second maxilla; (22) first foot, anterior; (23) second foot, posterior; (24) third foot, posterior; (25) second basipodal segment and first and second segments of endopod and exopod of third foot, anterior; (26) fourth foot, posterior; (27) second basipodal segment and first and second segments of endopod and exopod of fourth foot, anterior.

described two new species and presented descriptions of five hitherto unknown males. *Calocalanus gracilis* Tanaka, 1956, is not included in her revision.

Calocalanus plumulosus (Claus, 1863)

(PLATE 6, FIGS. 11–13)

Pacific records: Scott, 1909; Farran, 1929; 1936; Dakin and Colefax, 1940; Mori, 1942; Wilson, 1942; Anraku, 1953; Tanaka, 1953; Tanaka, 1956b; Heinrich, 1957b; 1958b; Yamazi, 1958a.

Vessel:	*Station*	*Occurrence*
Satsuma	32	2 females, 0.87 mm.

Remarks: According to Bernard's revision (see Remarks under preceding species), this species belongs to a new genus, *Leptocalanus*. The descriptions presented by Tanaka (1956b) and Bernard (1958) of the male are quite different and the two are not unispecific.

Family PSEUDOCALANIDAE

Clausocalanus arcuicornis (Dana, 1849)

(PLATE 7, FIGS. 1–6)

Pacific records: Vervoort, 1946; 1957. Also, Yamada, 1933; Johnson, 1942; Mori, 1942; Brodsky, 1950; Nakai, 1952; Anraku, 1954b; Tsuruta and Chiba, 1954b; Brodsky, 1955; Chiba, Tsuruta, and Maéda, 1955; Motoda and Anraku, 1955; Nagaya et al., 1955; Rose, 1955; Chiba, 1956; Tanaka, 1956b; Heinrich, 1957b; Honjo et al., 1957; Heinrich, 1958a; Yamazi, 1958a; Brodsky, 1959; Lindberg, 1959; Ponomareva, 1959.

Vessel:	*Station*	*Occurrence* (*measurement in mm.; number of specimens in paren.*)		
		f. *minor*, female	f. *major*, female	male
Hugh M. Smith	94	1.26–1.29 (2)		
Do	132	1.07–1.24 (17)		
Do	144	present	1.34–1.46 (8)	present.
Do	153	1.15–1.25 (4)	1.37 (1)	
Do	178	1.08–1.28 (21)	1.33 (1)	
Do	30		1.43–1.56 (14)	1.21–1.26 (2)
Do	31	1.19–1.31 (4)	1.42–1.53 (5)	
Do	63	1.33 (1)	1.51 (1)	
Stranger	34	1.16–1.28 (10)		
Orsom	10	1.16–1.24 (13)	1.53 (1)	
Horizon	32	1.14–1.24 (6)	1.30–1.46 (2)	
Satsuma	32	1.08–1.12 (3)		

Remarks: I have tentatively equated the females of this species to two forms which were described by Sewell, 1929. The two forms are distinguished by size and the total and relative lengths of the segments of the fifth feet. Forma *major* is large (1.30–1.60 mm.), and the fifth pair of feet is small (fig. 2). The distal segment is about twice as long as the proximal one (fig. 3). Forma *minor* is distinguished by its small size and its longer fifth feet (fig. 5). The distal and proximal segments are about equal in length.

Tanaka (1956b) has described two types of males of this species which differ in size and in the structure of the fifth feet. Although rare in the present collections, males with fifth feet referable to Tanaka's large form were found in the sample from the *Hugh M. Smith*, station 30.

Clausocalanus furcatus (Brady, 1883)

(PLATE 7, FIGS. 7–8)

Pacific records: Vervoort, 1946. Also, Mori, 1937; 1942; Wilson, 1942; Brodsky, 1950; Wilson, 1950; Nakai, 1952; Anraku, 1953; Tanaka, 1953; Yamazi, 1953c; Anraku, 1954b; Tsuruta and Chiba, 1954b; Motoda and Anraku, 1955; Nagaya et al., 1955; Rose, 1955; Chiba, 1956; Tanaka, 1956b; Honjo et al., 1957; Heinrich, 1958a.

Vessel:	*Station*	*Occurrence*
Hugh M. Smith	132	present.
Do	153	present.

Vessel:	Station	Occurrence
Do	178	2 females, 1.10, 1.12 mm.
Do	31	1 female, 1.14 mm.
Do	63	5 females, 1.00–1.17 mm.
Stranger	34	4 females, 1.12–1.19 mm.
Horizon	32	3 females, 1.02–1.19 mm.
Satsuma	32	1 female, 1.05 mm.

Remarks: This species is easily distinguished from the preceding by its short genital segment (fig. 7) and very small fifth feet (figs. 7, 8).

Family AETIDEIDAE

Euaetideus giesbrechti (Cleve, 1904)

(PLATE 7, FIGS. 9–27)

Pacific records: Vervoort, 1957. Also, as *Aetideus giesbrechti;* Johnson, 1942; Mori, 1942; Honjo, 1952; Anraku, 1954b; 1954c; Chiba, Tsuruta, and Maéda, 1955; Motoda and Anraku, 1955; Nagaya et al., 1955; Chiba, 1956; Honjo et al., 1957; Tanaka, 1957a; Yamazi, 1958a. As *Euaetideus giesbrechti*; Heinrich, 1957b; 1958a; 1958b.

Vessel:	Station	Occurrence
Hugh M. Smith	94	1 female, 1.95 mm.
Do	144	1 female, 1.95 mm.
Do	29	1 female, 1.97 mm.
Do	63	2 females, 1.97 mm.

Remarks: Vervoort (1957) has recently described a new species of *Euaetideus* (*E. australis*) as well as redescribed and figured the other three species (*E. giesbrechti, E. bradyi, E. acutus*) in this genus. The latter three species were represented in the present collections and as all three of them differ in a few details from Vervoort's descriptions, I have included a brief discussion and several figures of each of them. The chief differences between my specimens of *E. giesbrechti* and those described by Vervoort are listed below. The numbers in parenthesis are those given by Vervoort.

1. Second antennae (fig. 15). Four (3) setae on distal segment of exopod. Seven (6) setae on outer lobe and 9 (8) setae on inner lobe of endopod.
2. First maxillae (figs. 18–20). Second basal segment with 4 (5) setae. Second inner lobe with 3 (2) setae. Three (4) setae on the first segment of the endopod. It should be pointed out that Vervoort stated that the first maxilla of *E. giesbrechti* is like that of *E. australis.* The second basal segment of the first maxilla of the latter species is shown to have 4 setae, which agrees, in this respect, with the number on the present specimens.

The three species found in the present collections are distinguished by the shape of the anterior margin of the head (dorsal view); the character of the rostrum; and the posterior lateral thoracic margins. In *E. giesbrechti* the forehead is evenly rounded and the rostral plate is not visible (fig. 9). There are two small knobs between the rostral spines (fig. 14), and the posterior lateral thoracic margins have a characteristic shape (fig. 12). This species is also larger (1.95–2.00) than the other two.

Euaetideus acutus (Farran, 1929)

(PLATE 8, FIGS. 1–2)

Pacific records: Vervoort, 1957. Also, as *Aetideus acutus;* Tanaka, 1957a.

Vessel:	Station	Occurrence
Hugh M. Smith	94	5 females, 1.65–1.70 mm.
Do	132	2 females, 1.65, 1.70 mm.
Do	144	3 females, 1.70 mm.
Do	153	1 female, 1.70 mm.
Do	178	9 females, 1.55–1.65 mm.
Do	30	1 female, 1.61 mm.
Do	31	2 females, 1.55, 1.65 mm.
Do	63	1 female, 1.60 mm.
Stranger	34	1 female, 1.60 mm.

Remarks: Certain differences were noted in the second antennae and first maxillae of the present specimens and the descriptions and figures of these appendages given by Vervoort. These differences are summarized below:

1. Second antennae. Same as that described for *E. giesbrechti.* Vervoort shows 3 setae on the terminal segment of the exopod and 6 setae on the outer lobe and 8 setae on the inner lobe of the endopod.

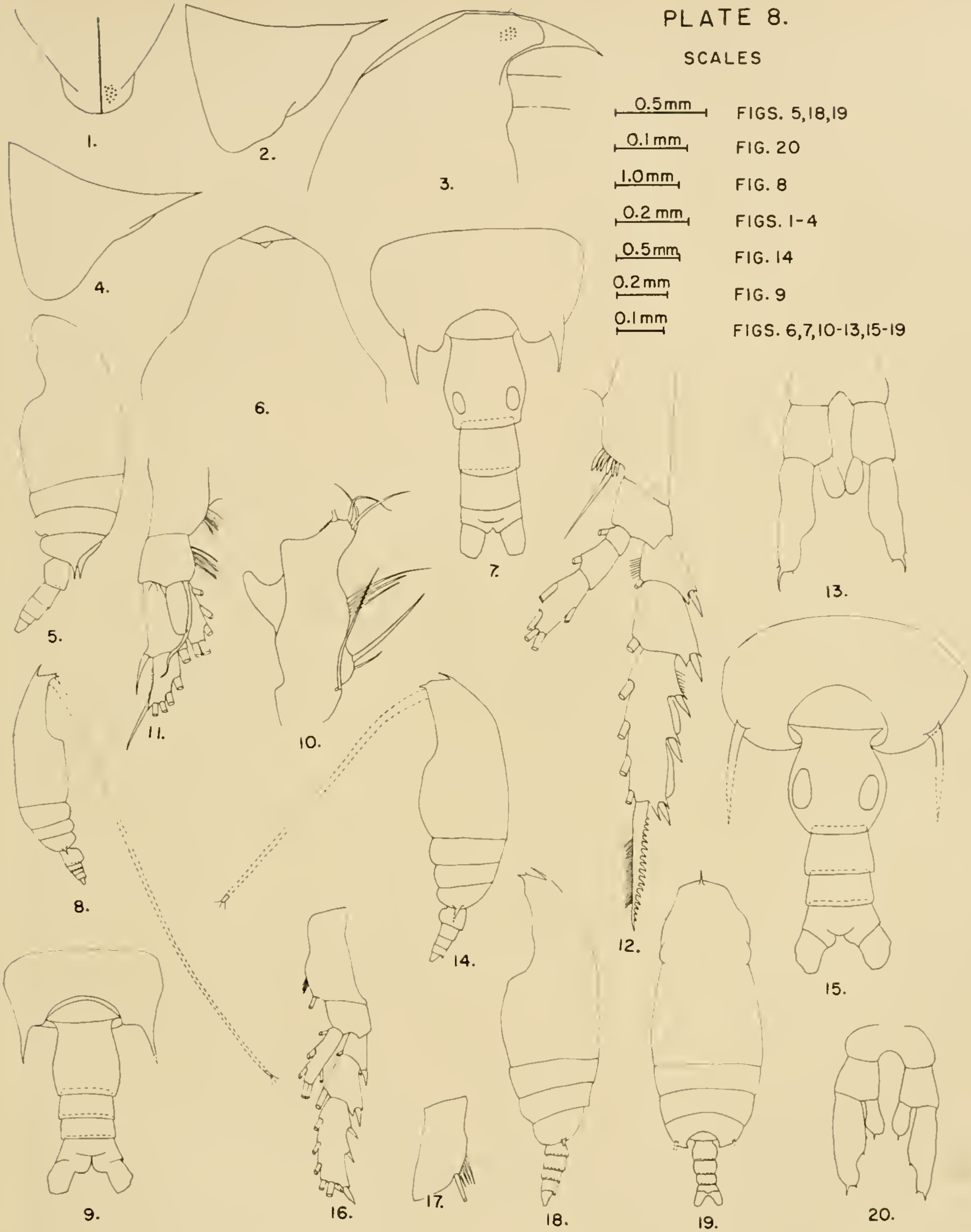

PLATE 8.—(1) *Euaetideus acutus*, female, forehead, dorsal view; (2) fourth and fifth thoracic segments, lateral view; (3) *E. bradyi*, female, forehead, lateral view; (4) fourth and fifth thoracic segments, lateral view; (5) *Chiridius poppei*, female, lateral view; (6) forehead, ventral view; (7) posterior part of thorax and abdomen, dorsal view; (8) *Gaetanus miles*, female, lateral view; (9) posterior part of thorax and abdomen, dorsal view; (10) first basipodal segment of maxilliped; (11) first foot; (12) fourth foot; (13) stage V, male, fifth pair of feet; (14) *Gaetanus minor*, female, lateral view; (15) posterior part of thorax and abdomen, dorsal view; (16) second foot; (17) first basipodal segment of fourth foot; (18) stage V, male, lateral view; (19) dorsal view; (20) fifth pair of feet.

2. First maxillae. Same as that described for *E. giesbrechti.* Vervoort shows 5 setae on the second basal segment, 2 setae on the second inner lobe and 4 setae on the first segment of the endopod.

E. acutus may be identified by the large rostral plate which is visible in dorsal view (fig. 1) and the character of the posterior lateral thoracic margins (fig. 2).

Euaetideus bradyi (A. Scott, 1909)

(Plate 8, figs. 3–4)

Pacific records: Vervoort, 1957; Also, as *Aetideus bradyi;* Tanaka, 1957a.

Vessel:	Station	Occurrence
Hugh M. Smith	94	12 females, 1.60–1.65 mm.
Do	144	3 females, 1.65 mm.
Do	63	1 female, 1.70 mm.

Remarks: The second antennae differ from that figured by Vervoort in the manner described above for *E. giesbrechti.* The first maxilla of the present specimens has 4 setae on the basal segment and 3 setae on the second inner lobe. Vervoort showed 5 and 2 setae, respectively, on these parts of the maxilla. The anterior margin of the head of this species appears to be pitted similar to that of the preceding two species.

E. bradyi is distinguished from the above two species by the absence of knobs between the rostral spines and the character of the posterior lateral thoracic margins (fig. 4). In lateral view, a short hair is visible just dorsad of the base of the rostrum. I have not observed this hair in the other two species.

Chiridius poppei Giesbrecht, 1892

(Plate 8, figs. 5–7)

Pacific records: Scott, 1909; Farran, 1929; Tanaka, 1937; Wilson, 1942; Brodsky, 1950; Tanaka, 1953; 1957a.

Vessel:	Station	Occurrence
Hugh M. Smith	94	2 females, 1.59, 1.83 mm.
Do	63	1 female, 1.70 mm.

Remarks: This species was found in two samples collected in the eastern Pacific. Vervoort (1957) suggested that *C. poppei* and *C. gracilis* Farran, 1905 may represent different size groups of the same species. He has also indicated how the two forms differ.

Gaetanus miles Giesbrecht, 1888

(Plate 8, figs. 8–13)

Pacific records: Scott, 1909; Farran, 1936; Wilson, 1942; Brodsky, 1950; Tanaka, 1953; 1957b. As *G. secundus* Esterly, 1911; Johnson, 1942.

Vessel:	Station	Occurrence
Hugh M. Smith	29	2 females, 3.40, 3.50 mm.
Do	63	2 females, 3.52 mm.; 1 male (stage V), 2.89 mm.

Remarks: The female of this species is easily recognized by the elongate antennae which exceed the furca by the last 9 segments. Accompanying the females in the collection from *Smith* 63 was an immature male (stage V) which is apparently referable to this species. The fifth feet are shown in figure 13. The adult male is undescribed, although Esterly (1911) mentions that he has observed this sex, presumably in company with the females of his *G. secundus* (=*G. miles*).

Gaetanus minor Farran, 1905

(Plate 8, figs. 14–20)

Pacific records: Vervoort, 1957. Also, Anraku, 1954b; 1954c; Tanaka, 1957b; Heinrich, 1958b.

Vessel:	Station	Occurrence
Hugh M. Smith	29	2 females, 2.18 mm.
Do	63	2 females, 2.15, 2.24 mm.; 1 male (stage V), 1.87 mm.
Horizon	32	1 female, 2.00 mm.

Remarks: The female is distinguished from *G. miles* by the short antennae and the presence of numerous small spines (fig. 17) on the first basipodal segment of the fourth feet. Rose (1933) states that the endopods of the second feet are composed of 2 segments. These endopods of the present specimens, as well as the one figured by Scott (1909), consist of only 1 segment (fig. 16). Associated with the females in the collection from *Smith* 63 was a juvenile

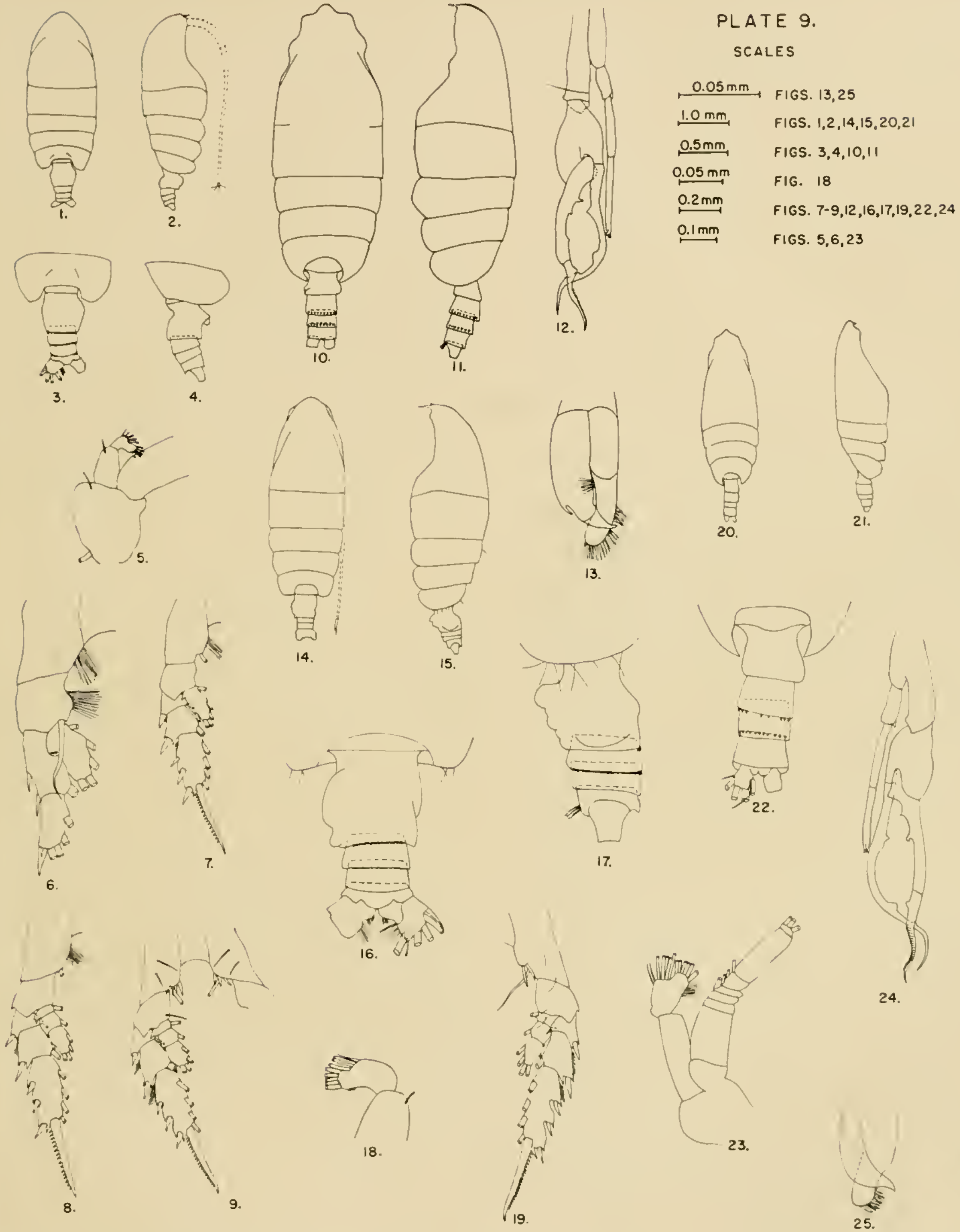

Plate 9.—(1) *Euchirella bella*, female, dorsal view; (2) lateral view; (3) posterior part of thorax and abdomen, dorsal view; (4) posterior part of thorax and abdomen, lateral view; (5) endopod of second antenna; (6) first foot; (7) second foot; (8) third foot; (9) fourth foot; (10) male, dorsal view; (11) lateral view; (12) fifth pair of feet; (13) terminal part of left fifth foot; (14) *E. venusta*, female, dorsal view; (15) lateral view; (16) abdomen, dorsal view; (17) abdomen, lateral view; (18) endopod of second antenna; (19) fourth foot; (20) male, dorsal view; (21) lateral view; (22) abdomen, dorsal view; (23) second antenna; (24) fifth pair of feet; (25) terminal part of left fifth foot.

male (stage V), which is apparently referable to this species (figs. 18–20). The male of this species has been hitherto unknown.

Euchirella bella Giesbrecht, 1888

(PLATE 9, FIGS. 1–13)

Pacific records: Vervoort, 1949; Wilson, 1950.

Vessel:	Station	Occurrence
Hugh M. Smith	153	2 females, 3.90, 4.18 mm.; 1 male, 3.33 mm.
Do	31	2 females, 3.80 mm.; 1 male, 3.36 mm.
Do	63	1 female, 3.80 mm.
Stranger	34	1 female, 3.80 mm.

Remarks: The species of female *Euchirella* are distinguished by the shape of the genital segment, number of setae on the endopod of the second antennae and the spination of the first basipodal segment of the fourth pair of feet. The males are identified by the structure of the fifth feet. The genital segment of *E. bella* is nearly symmetrical in dorsal view (figs. 1, 3) and is produced in ventral view (figs. 2, 4). The second segment of the endopod of the second antennae in the specimens examined has 5 setae on the outer and 5 setae on the inner lobe (fig. 5). Giesbrecht and Schmeil (1898) state that there are 6 and 5 setae on these respective lobes. The males in the present collections have 6 setae on the external lobe and 7 on the internal lobe, the 2 most internal ones being very small and slender. Vervoort (1949) indicated that there were 6 setae on each lobe. The number of spines on the first basipodal segment of the fourth feet is variable. Some specimens have 5 on each side and others have 4 on one side and 3 on the other (fig. 9). Scott (1909) and Sewell (1947) have also noted a variable number of spines on this segment.

Wilson (1950) has erroneously synonymized *E. amoena* with this species. See discussion of this under *E. amoena* below.

Euchirella venusta Giesbrecht, 1888

(PLATE 9, FIGS. 14–25)

Pacific records: Scott, 1909; Farran, 1929; Vervoort, 1949; Wilson, 1950; Tanaka, 1953; 1957b.

Vessel:	Station	Occurrence
Hugh M. Smith	63	4 females, 4.37–4.84 mm.; 1 male, 3.80 mm.

Remarks: The female is identified by the knob-like protrusion from the left posterior margin of the genital segment (fig. 16); the presence of 4 setae on the inner lobe and 5 setae on the external lobe of the endopod of the second antennae (fig. 18); and the two long spines on the first basipodal segments of the fourth pair of feet. Sewell (1947) has recently described the male, additional figures of which are given herein (figs. 20–25). The second antennae (fig. 23) have 6 setae on the outer lobe and 7 setae on the inner lobe, 2 of which are small. Sewell reported 6 setae on each lobe. The structure of the fifth feet agrees quite well with Sewell's figure of this appendage.

Euchirella pulchra (Lubbock, 1856)

(PLATE 10, FIGS. 1–4)

Pacific records: Esterly, 1905; Scott, 1909; Johnson, 1942; Wilson, 1942; Davis, 1949; Vervoort, 1949; Brodsky, 1950; Wilson, 1950; Tanaka, 1953; 1957b.

Vessel:	Station	Occurrence
Hugh M. Smith	63	1 female, 3.42 mm.

Remarks: The genital segment is produced into a rounded swelling to the left (fig. 2). The second segment of the endopod of the second antennae has 6 setae on each lobe (fig. 3). This is the number reported also by Tanaka (1957b), but Giesbrecht and Schmeil (1898) and Vervoort (1952) stated that the internal lobe has 5 setae. Possibly the very small, innermost seta on the internal lobe was overlooked. An additional identification character is the presence of 2 spines on the first basipodal segment of the fourth pair of feet (fig. 4).

Euchirella amoena Giesbrecht, 1888

(PLATE 10, FIGS. 5–10)

Synonymy

Euchirella amoena Giesbrecht, 1888, Atti Acc. Lincei. Rend., Ser. 4, 4, sem. 2: 336.

Euchirella brevis, Sars, 1905. Bull. Mus. Oceanogr., Monaco, 26: 12.

Euchirella bella (partim), Wilson, 1950, U.S.N.M., Bull. 100, 14: 218.

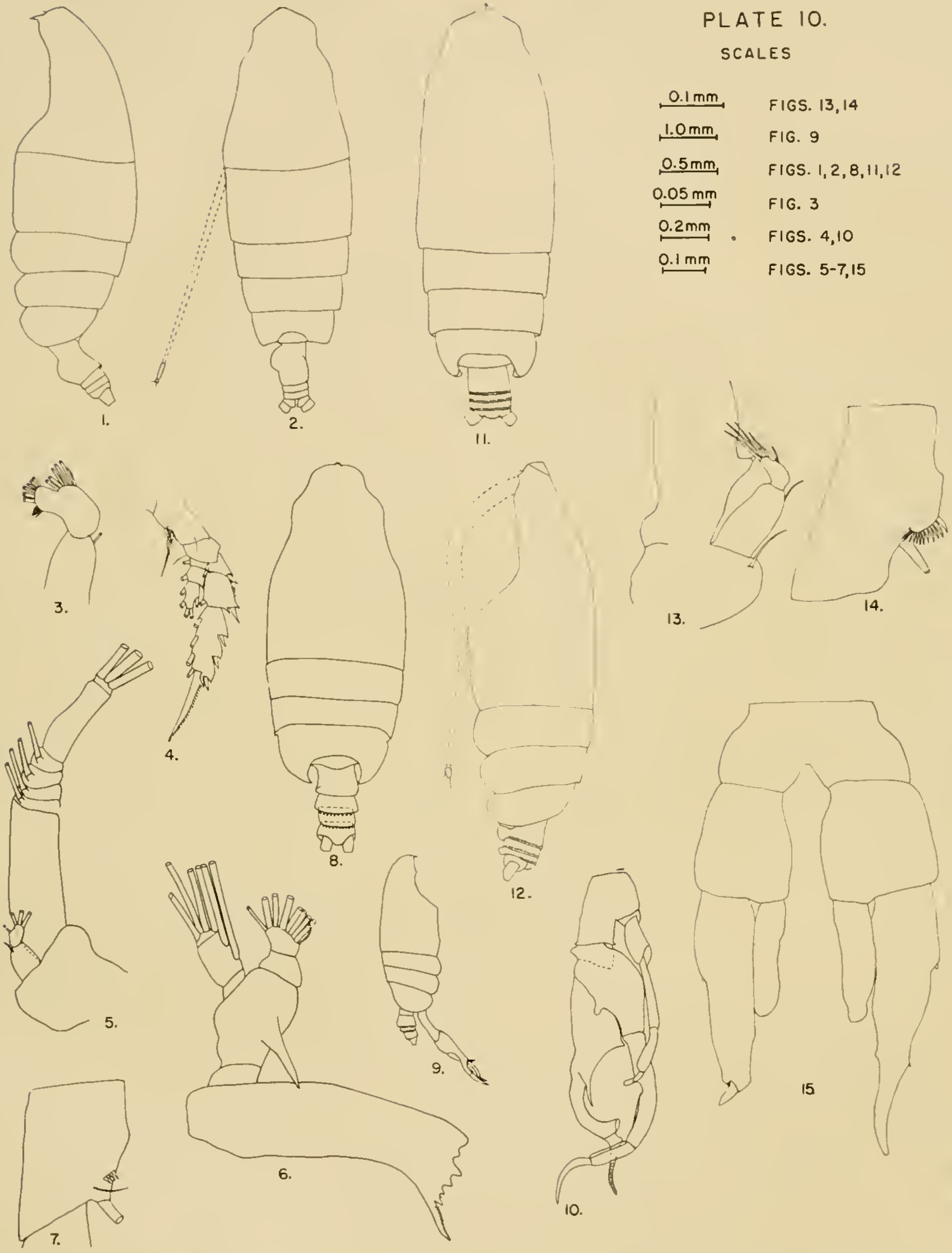

Plate 10.—(1) *Euchirella pulchra*, female, lateral view; (2) dorsal view; (3) endopod of second antenna; (4) fourth foot; (5) *E. amoena*, female, second antenna; (6) mandible: (7) first basipodal segment of fourth foot; (8) male, dorsal view; (9) lateral view; (10) fifth pair of feet; (11) *E. curticauda*, female, dorsal view; (12) lateral view; (13) endopod of second antenna; (14) first basipodal segment of fourth foot; (15) *E. maxima*, stage V, male, fifth pair of feet.

Pacific records: Esterly, 1905; Scott, 1909; Farran, 1929; Mori, 1937; Wilson, 1942; Brodsky, 1950; Wilson, 1950; Tanaka, 1953; Chiba, Tsuruta, and Maéda, 1955; Nagaya et al., 1955; Chiba, 1956; Tanaka, 1957b; Yamazi, 1958a.

Vessel:	*Station*	*Occurrence*
Hugh M. Smith	132	1 male, 3.20 mm.
Do	144	1 female, 3.70 mm.
Do	153	2 females, 3.61, 3.70 mm.; 3 males, 3.33 mm.
Do	178	1 female, 3.80 mm.
Do	63	1 male, 3.33 mm.

Remarks: Fleminger (1956) is no doubt correct in placing Sars' (1905) *brevis* (described from female) in synonymy with Giesbrecht's (1888) *amoena* (described from male). This synonymy is further substantiated by Mori's (1937) description of the female of *amoena*. Although Mori did not describe the fourth pair of feet, the total length, abdomen-cephalothorax ratio, length of the first antennae, length of the endopod of the second antennae and the number of setae on the distal segment of the endopod of the second antennae clearly establish that Mori's *E. amoena* and Sars' *E. brevis* are unispecific.

As Fleminger has stated, Wilson's synonymy of *E. amoena* under *E. bella* is an error. The male of *E. bella* was described by Sewell (1947) and Vervoort (1949); neither author was cited by Wilson. It should be noted, however, that Dr. Wilson's paper was published nine years after his death.

Euchirella curticauda Giesbrecht, 1888

(PLATE 10, FIGS. 11–14)

Pacific records: Esterly, 1906; Scott, 1909; Johnson, 1942; Mori, 1942; Wilson, 1942; Davis, 1949; Brodsky, 1950; Wilson, 1950; Anraku, 1952; Tanaka, 1953; 1957b.

Vessel:	*Station*	*Occurrence*
Orsom	10	2 females, 3.52, 3.62 mm.

Remarks: This species is recognized by the presence of a crest, absence of a rostrum (fig. 12) and the presence of a comb of spines on the first basipodal segment of the fourth pair of feet (fig. 14).

Euchirella maxima Wolfenden, 1905

(PLATE 10, FIG. 15)

Pacific records: Scott, 1909; Wilson, 1950.

Vessel:	*Station*	*Occurrence*
Hugh M. Smith	29	1 female (stage V), 5.79 mm.; 1 male (stage V), 5.70 mm.

Remarks: A male and female were obtained in the 500 m. collection made at the above station. Both sexes have a crest on the forehead. Sewell (1929) has described the stage V individuals of this species.

Pseudochirella sp.

Vessel:	*Station*	*Occurrence*
Hugh M. Smith	29	4 juveniles, 6.93–7.14 mm.

Remarks: These large juvenile copepods could not be assigned to a species. They were obtained from the 500–meter plankton tow.

Chirundina streetsi Giesbrecht, 1895

(PLATE 11, FIGS. 1–4)

Pacific records: Esterly, 1906; Scott, 1909; Farran, 1929; Johnson, 1942; Brodsky, 1950; Wilson, 1950; Tanaka, 1953; 1957b.

Vessel:	*Station*	*Occurrence*
Horizon	32	1 female, 4.94 mm.

Remarks: This species is distinguished from the following one by its large size, pronounced crest on forehead (fig. 1), and the presence of 2 spines on the first exopodal segment of the first feet (fig. 4).

Chirundina indica Sewell, 1929

(PLATE 11, FIGS. 5–20)

Pacific records: None.

Vessel:	*Station*	*Occurrence*
Hugh M. Smith	63	1 female, 4.66 mm.

Remarks: I have compared in some detail (figs. 5–20) the present species with the descriptions of *C. indica* provided by Sewell (1929, 1947). On the basis of his description the latter species is distinguished from *C.*

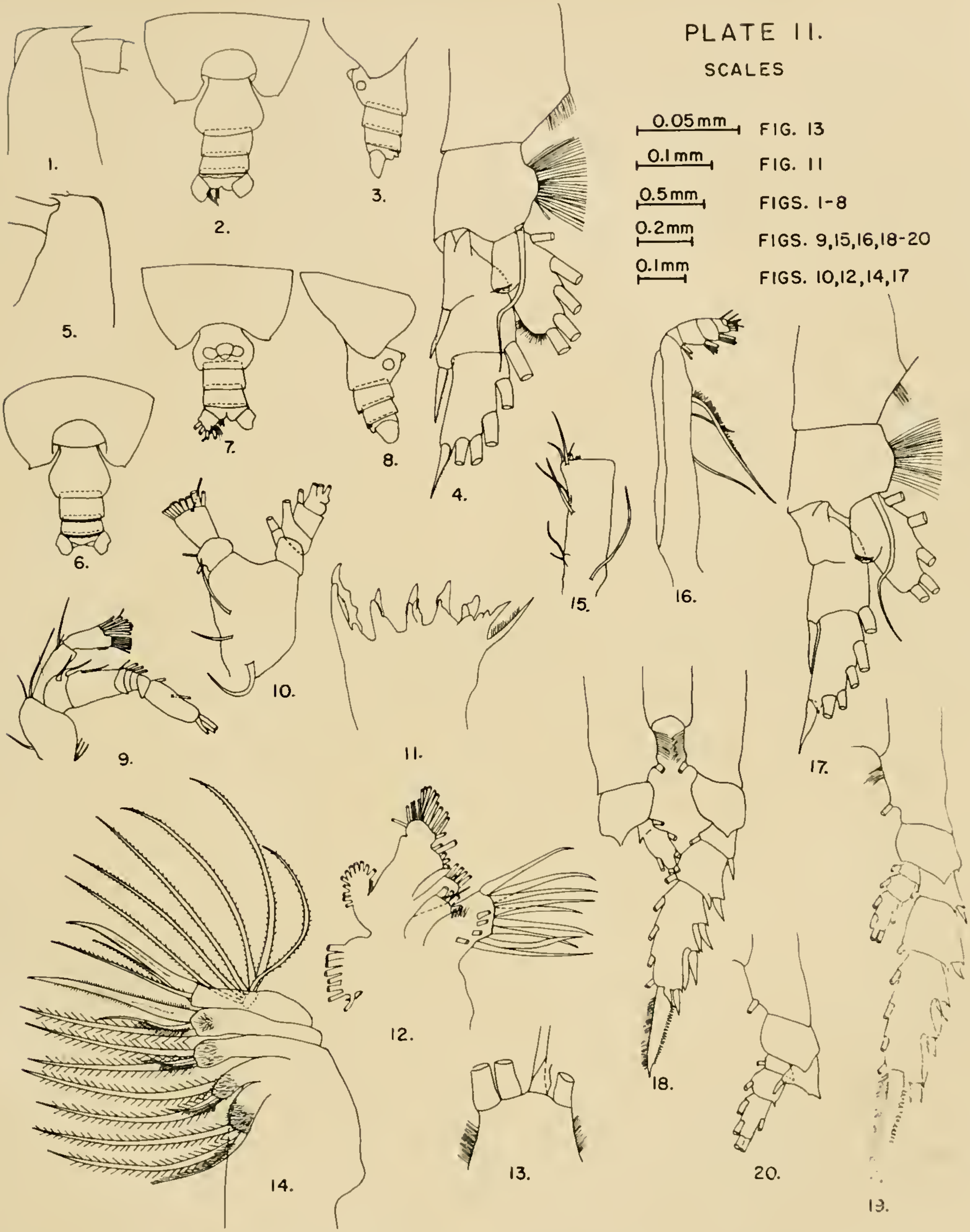

Plate 11.—(1) *Chirundina streetsi*, female, forehead, lateral view; (2) posterior part of thorax and abdomen, dorsal view; (3) abdomen, lateral view; (4) first foot; (5) *C. indica*, forehead, lateral view; (6) posterior part of thorax and abdomen, dorsal view; (7) posterior part of thorax and abdomen, ventral view; (8) posterior part of thorax and abdomen, lateral view; (9) second antenna; (10) mandible palpus; (11) gnathal lobe of mandible; (12) first maxilla; (13) terminal part of third inner lobe of first maxilla; (14) second maxilla; (15) first basipodal segment of maxilliped; (16) distal part of maxilliped; (17) first foot; (18) second pair of feet (one exopod and one endopod missing); (19) third foot; (20) fourth foot (distal part of exopod missing).

PLATE 12.

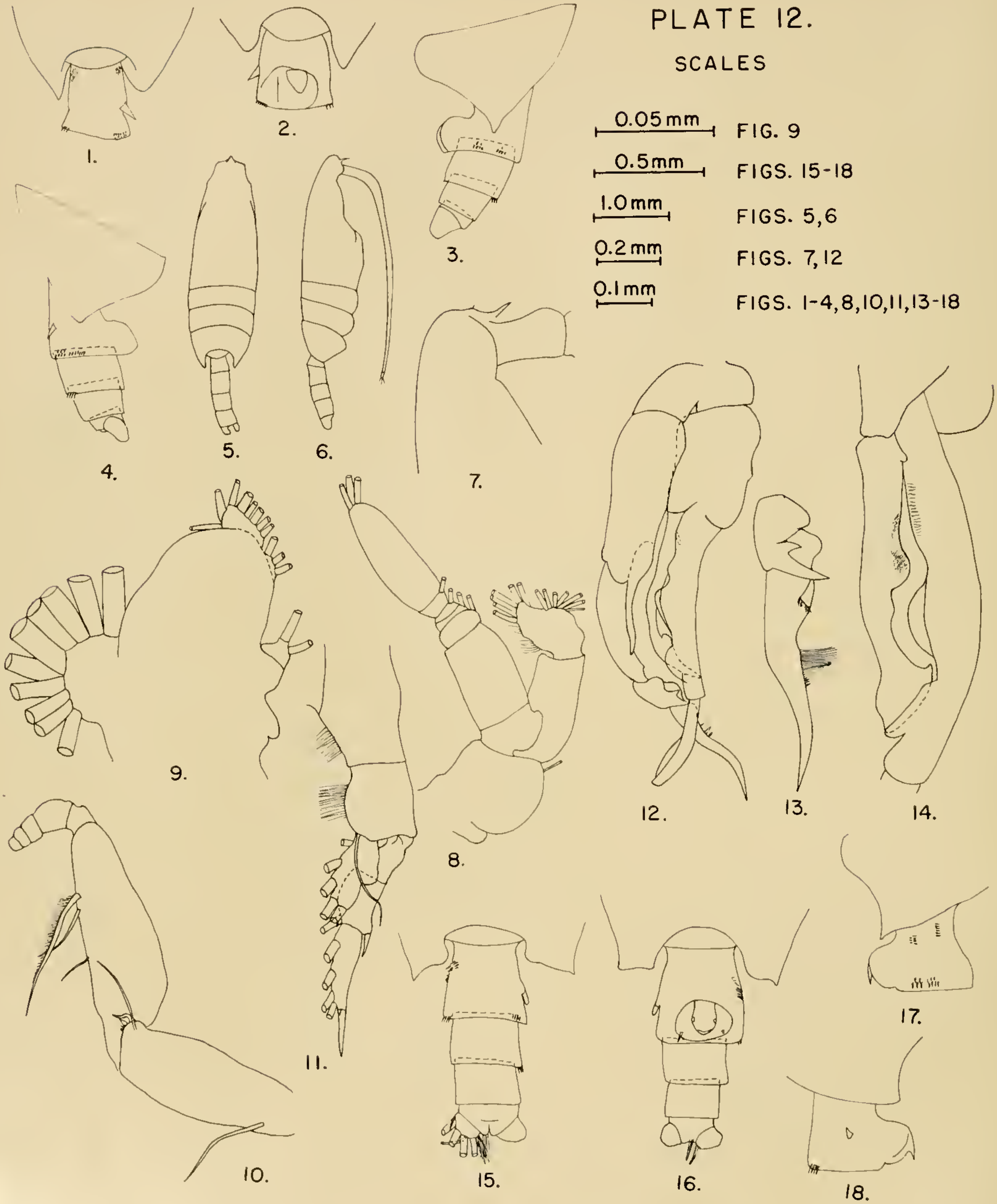

PLATE 12.—(1) *Undeuchaeta plumosa*, female, genital segment, dorsal view; (2) ventral view; (3) posterior part of thorax and abdomen, left side; (4) posterior part of thorax and abdomen, right side; (5) male, dorsal view; (6) lateral view; (7) forehead, lateral view; (8) second antenna; (9) first maxilla (part); (10) maxilliped (setae on distal part omitted); (11) first foot; (12) fifth pair of feet; (13) terminal part of left fifth foot; (14) right fifth foot (part); (15) *U. intermedia*, female, dorsal view; (16) abdomen, ventral view; (17) genital segment, left side; (18) genital segment, right side.

streetsi by its low crest, the smoothly rounded posterior thoracic margins and the presence of but 1 external spine on the first exopodal segment of the first feet. Except for the posterior thoracic margins, which have 1 small projection (figs. 7–9), my specimen agrees with Sewell's *indica*. In details of the mouth parts, two minor differences were noted. Sewell's specimens have 6 setae on the outer lobe of the second antenna, while the present specimen has 7 (fig. 10); the exopod of the mandible has 9 setae (Sewell probably referred to the distal segment); the present specimen has 10, one of which is extremely small (fig. 11).

The projections on the posterior thoracic margins may be a variable character as Vervoort (1957) has observed in several species of a related genus, *Undeuchaeta*. It seems best therefore to refer the present species to *C. indica*.

Undeuchaeta plumosa (Lubbock, 1856)

(PLATE 12, FIGS. 1–14)

Pacific records: Vervoort, 1957. Also, Brodsky, 1950; Heinrich, 1957b; Tanaka, 1957b.

Vessel:	*Station*	*Occurrence*
Hugh M. Smith	63	1 male, 3.52 mm.
Horizon	32	1 female, 3.47 mm.
Satsuma	32	1 female, 3.41 mm.

Remarks: The female is distinguished by the presence of a spine on the right side of the genital segment (figs. 1, 2) near the dorsal surface, and the male by the structure of the fifth feet (figs. 12–14).

Undeuchaeta intermedia A. Scott, 1909

(PLATE 12, FIGS. 15–18)

Pacific records: Vervoort, 1957. Also, Johnson, 1942; Brodsky, 1950 (as *U. bispinosa*)

Vessel:	*Station*	*Occurrence*
Hugh M. Smith	63	4 females, 3.99–4.28 mm.
Horizon	32	3 females, 3.99–4.08 mm.

Remarks: The large ventral spine-like protrusion of the genital segment in the female (figs. 17, 18) distinguishes this species from the preceding one.

Family EUCHAETIDAE

Euchaeta marina (Prestandrea, 1833)

(PLATE 13, FIG. 1)

Pacific records: Scott, 1909; Marukawa, 1921; Yamada, 1933b; Mori, 1937; Dakin and Colefax, 1940; Mori, 1942; Wilson, 1942; Brodsky, 1950; Motoda, Iizuka, and Anraku, 1950; Wilson, 1950; Anraku, 1952; Honjo, 1952; Nakai, 1952; Anraku, 1953; Chiba, 1953b; Tanaka, 1953; Anraku, 1954b; Tsuruta and Chiba, 1954b; Chiba, Tsuruta, and Maéda, 1955; Motoda and Anraku, 1955; Nagaya et al., 1955; Rose, 1955; Chiba, 1956; Heinrich, 1957b; Honjo et al., 1957; Gilmartin, 1958; Heinrich, 1958a; Tanaka, 1958; Yamazi, 1958a; Lindberg, 1959.

Vessel:	*Station*	*Occurrence*
Hugh M. Smith	132	1 male, 3.12 mm.
Do	144	1 female, 3.61 mm.
Do	153	2 females, 3.32, 3.42 mm.
Do	178	1 female, 3.06 mm.
Do	30	3 females, 2.96–3.06 mm.;1 male, 2.99 mm.
Do	31	present.
Do	63	4 females, 3.40–3.60 mm.; 1 male, 3.37 mm.
Stranger	34	4 females, 3.13–3.26 mm.; 5 males, 3.06–3.23 mm.
Orsom	10	3 females, 3.13–3.23 mm.
Horizon	32	2 females, 3.13, 3.23 mm.

Remarks: This is probably the most widespread species in the genus. It occurred in ten of the present samples and in two (*Smith* 153 and 30), it comprised a fairly significant percentage of the total number of copepods.

Euchaeta wolfendeni A. Scott, 1909

(PLATE 13, FIGS. 2–9)

Pacific records: Farran, 1936; Mori, 1937; Wilson, 1950; Honjo, 1952; Tanaka, 1953; Tsuruta and Chiba, 1954b; Chiba, Tsuruta, and Maéda, 1955; Nagaya et

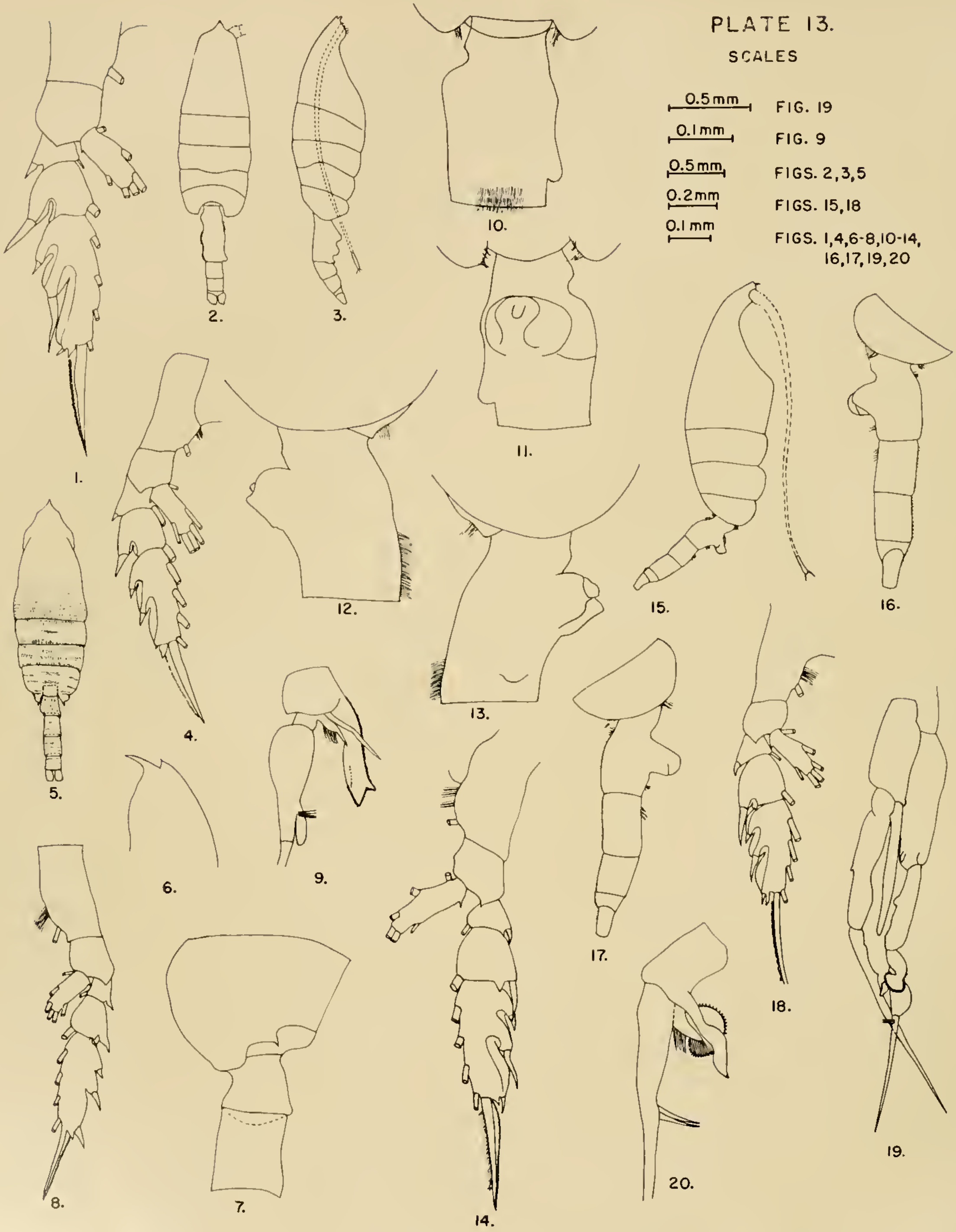

PLATE 13.—(1) *Euchaeta marina*, female, second foot; (2) *E. wolfendeni*, female, dorsal view; (3) lateral view; (4) second foot; (5) male, dorsal view; (6) forehead, lateral view; (7) posterior part of thorax and first two abdominal segments, lateral view; (8) second foot; (9) terminal part of left fifth foot; (10) *E. media*, female, genital segment, dorsal view; (11) genital segment, ventral view; (12) genital segment, left side; (13) genital segment, right side; (14) second foot; (15) *E. tenuis*, female, lateral view; (16) posterior part of thorax and abdomen, left side; (17) posterior part of thorax and abdomen, right side; (18) second foot; (19) male, fifth pair of feet; (20) terminal part of left fifth foot.

al., 1955; Chiba, 1956; Honjo et al., 1957; Tanaka, 1958; Yamazi, 1958a.

Vessel:	*Station*	*Occurrence*
Hugh M. Smith	132	1 female, 2.50 mm.
Do	63	1 female, 2.52 mm.
Stranger	34	3 females, 2.24–2.38 mm.; 2 males, 2.21, 2.35 mm.
Horizon	32	1 female, 2.55 mm.; 3 males, 2.31–2.44 mm.
Satsuma	32	2 females, 2.38, 2.40 mm.; 1 male, 2.31 mm.

Remarks: The female is distinguished by the long genital segment, the right posterior margin of which is produced into a rounded knob (fig. 2). The relative lengths of the outer-edge spines on the second and third exopodal segments of the second feet (fig. 4) are also diagnostic (cf. *E. marina*, plate 13, fig. 1). The male is identified by the structure of the terminal part of the left fifth foot (fig. 9).

Euchaeta media Giesbrecht, 1888

(PLATE 13, FIGS. 10–14)

Pacific records: Vervoort, 1957. Also, Johnson, 1942; Brodsky, 1950; Tsuruta and Chiba, 1954b; Chiba, Tsuruta, and Maéda, 1955; Nagaya et al., 1955; Heinrich, 1957b; Honjo et al., 1957; Tanaka, 1958.

Vessel:	*Station*	*Occurrence*
Hugh M. Smith	63	1 female, 3.52 mm.

Remarks: The female of *E. media* is recognized by the characteristic swelling on the left side and the knob-like protrusion on the right side of the genital segment (figs. 10, 11). The middle spine on the outer edge of the third exopodal segment of the second pair of feet is elongate and the spine on the second exopodal segment reaches beyond the base of the proximal spine on the third segment (fig. 14).

Euchaeta tenuis Esterly, 1906

(PLATE 13, FIGS. 15–20)

Pacific records: Esterly, 1906; Scott, 1909; Brodsky, 1950. As *E. solida*, Esterly, 1911.

Vessel:	*Station*	*Occurrence*
Hugh M. Smith	29	4 females, 5.60–5.98 mm.; 3 males, 5.03–5.22 mm.
Do	63	1 female, 5.13 mm.; 1 male, 4.75 mm.
Do	32	present.

Remarks: The large and asymmetrical ventral protrusions (figs. 16, 17) of the female genital segment will identify this species. The outer-edge spines of the second pair of feet (fig. 18) are also diagnostic. In the male the structure of the second segment of the left fifth foot (figs. 19, 20) is characteristic. It is dilated and coarsely serrate.

Euchaeta concinna Dana, 1849

(PLATE 14, FIGS. 1–13)

Synonymy:

Euchaeta consimilis Farran, 1936, Great Barrier Reef Exped. 1928–29. Sci. Rept. 5(3): 90.

Pacific records: Scott, 1909; Farran, 1936; Mori, 1937; Dakin and Colefax, 1940; Wilson, 1950; Tanaka, 1953; Rose, 1955; Honjo et al., 1957; Heinrich, 1958b; Tanaka, 1958. As *E. consimilis;* Farran, 1936; Rose, 1955.

Vessel:	*Station*	*Occurrence*
Satsuma	32	3 females, 2.52–2.55 mm.; 1 male, 2.24 mm.

Remarks: Farran (1936) described *E. consimilis* from 4 female specimens collected near the Great Barrier Reef. He also found *E. concinna* in his collections, but this species was observed only inside the reef where it was one of the most characteristic of the copepods. According to Farran, *consimilis* differs, morphologically, from *concinna* in the form of the protrusion on the right side of the genital segment in the female (see Farran's fig. 6) and in size. As Farran pointed out, Sewell (1929) observed "a considerable degree of variation" in the form of the genital protrusion in *concinna* collected in the Indian Ocean. The latter author suggested that this variation may be correlated with egg laying which causes the protrusion to increase in size.

The size of specimens, as recorded in the literature is also variable.

Source:	*Female*	*Male*
Mori, 1937 (Japan)	3.0 mm.	
Tanaka, 1958 (Japan)	2.87–3.25 mm.	

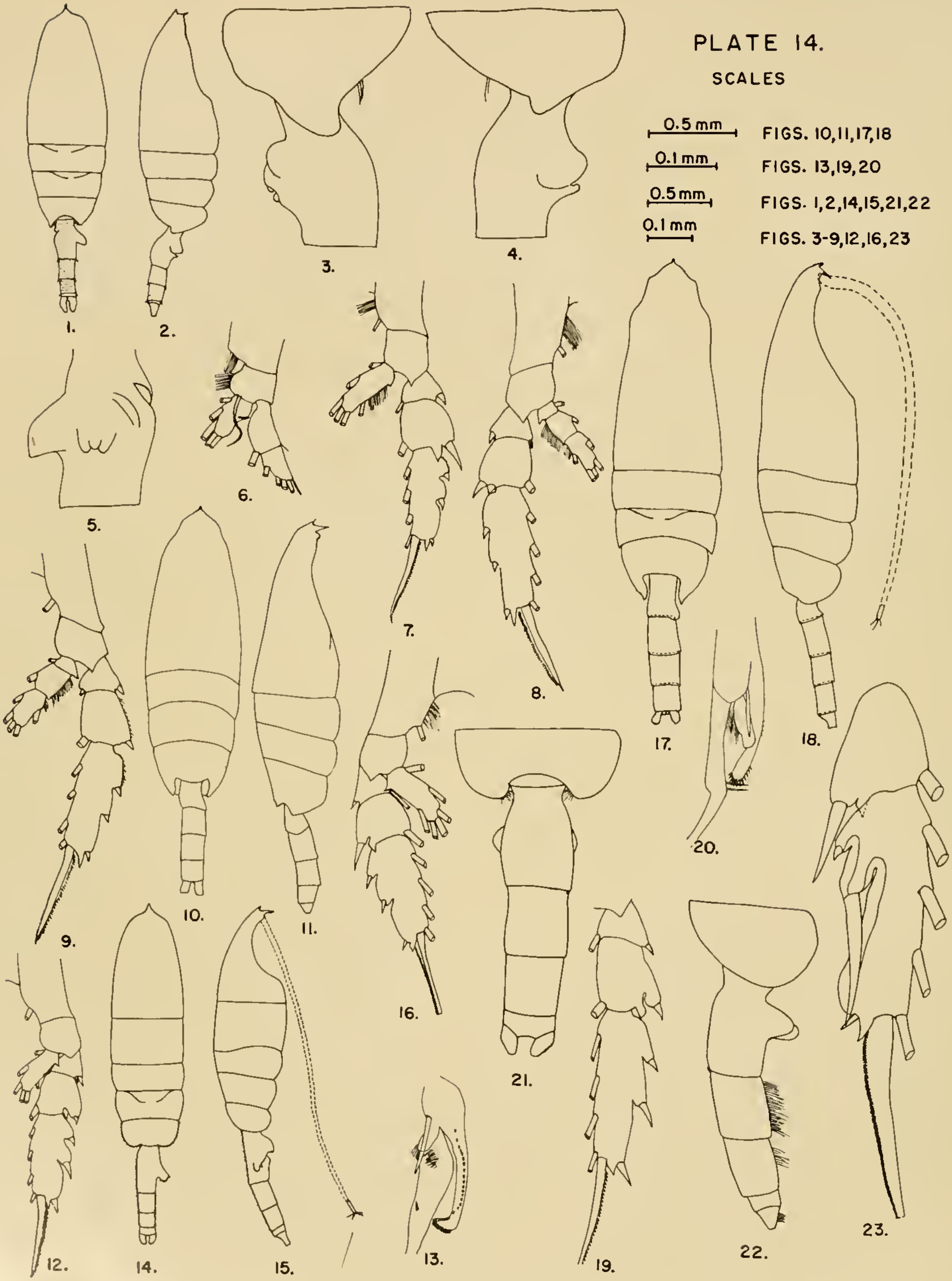

PLATE 14.—(1) *Euchaeta concinna*, female, dorsal view; (2) lateral view; (3) posterior part of thorax and genital segment, left side; (4) posterior part of thorax and genital segment, right side; (5) genital segment, ventral side; (6) first foot; (7) second foot; (8) third foot; (9) fourth foot; (10) male, dorsal view; (11) lateral view; (12) second foot; (13) terminal part of left fifth foot; (14) *E. longicornis*, female, dorsal view; (15) lateral view; (16) second foot; (17) male, dorsal view; (18) lateral view; (19) exopod of second foot; (20) terminal part of left fifth foot; (21) *E. spinosa*, female, posterior part of thorax and abdomen, dorsal view; (22) lateral view; (23) second and third segments of exopod of second foot.

Vessel:	*Station*	*Occurrence*
Giesbrecht and Schmeil, 1898 (tropical Pacific)	3.3 mm.	2.75 mm.
Heinrich, 1958b (tropical Pacific)	2.5 mm.	
Farran, 1936 (inside Barrier Reef)	3.25–3.40 mm.	2.54–2.76 mm.
Farran, 1936 (outside Barrier Reef)	2.36–2.67 mm.	
Dakin and Colefax, 1940 (Australia)	3.75 mm.	2.6 mm.
Sewell, 1929 (Indian Ocean)	2.5–3.5 mm.	2.4–3.0 mm.
Wolfenden, 1905 (Indian Ocean)	2.75–3.0 mm.	

In view of the wide size range in both sexes and the variable nature of the genital segment in the female, it seems best to consider *E. consimilis* as a synonym of *E. concinna*.

Euchaeta longicornis Giesbrecht, 1888

(Plate 14, figs. 14–20)

Pacific records: Scott, 1909; Farran, 1929; 1936; Mori, 1937; Wilson, 1950; Honjo, 1952; Nakai, 1952; Tanaka, 1953; Anraku, 1954b; Chiba, Tsuruta, and Maéda, 1955; Nagaya et al., 1955; Honjo et al., 1957; Tanaka, 1958.

Vessel:	*Station*	*Occurrence*
Hugh M. Smith	94	3 females, 2.88 mm.
Do	132	8 females, 2.65–2.92 mm.; 1 male, 2.65 mm.

Remarks: The female genital segment has a large protrusion on the right side from which arises a smaller spine-like process.

Wilson (1950) described the male sex of this species. I have compared my single male specimen (except the body, which was destroyed in dissection) to one identified by G. O. Sars and loaned to me by the U.S. National Museum. The two are unispecific. In the Museum specimen a small spine is present on the superior-lateral margins of the fifth thoracic segment as is also found on the male of *E. wolfendeni* (see plate 13, fig. 7). I probably overlooked these spines in my specimen and therefore they are not shown in the figure given of the male (fig. 18).

Euchaeta spinosa Giesbrecht, 1892

(Plate 14, figs. 21–23)

Pacific records: Esterly, 1905; Johnson, 1942; Brodsky, 1950; Wilson, 1950; Tanaka, 1953; 1958. As male of *Undeuchaeta major;* Esterly, 1905.

Vessel:	*Station*	*Occurrence*
Hugh M. Smith	29	1 female, 6.94 mm.

Remarks: The ventral projections of the genital segment (fig. 22) are visible in dorsal view. The middle spine on the outer margin of the third exopodal segment of the second feet is greatly elongate, and the spine on the second exopodal segment surpasses the tip of the first spine on the third segment (fig. 23).

Family PHAENNIDAE

Phaenna spinifera Claus, 1863

(Plate 15, fig. 1)

Pacific records: Scott, 1909; Farran, 1929; Mori, 1937; Wilson, 1942; 1950; Tanaka, 1953; Anraku, 1954b; 1954c; Tsuruta and Chiba, 1954b; Chiba, Tsuruta, and Maéda, 1955; Motoda and Anraku, 1955; Nagaya et al., 1955; Chiba, 1956; Honjo et al., 1957; Yamazi, 1958a. As *Onchocalanus nudipes;* Wilson, 1942.

Vessel:	*Station*	*Occurrence*
Hugh M. Smith	94	present.
Do	132	3 females, 1.87–1.90 mm.
Do	31	1 female, 1.60 mm.
Do	63	present.
Orsom	10	1 female, 1.87 mm.
Horizon	32	present.

Remarks: The globular thorax, small abdomen, and lack of fifth feet (in the female) make this species easily recognized. Vervoort (1950) placed Wilson's *Onchocalanus nudipes* in synonymy with *Phaenna spinifera.*

Xanthocalanus dilatus n. sp.

(Plate 15, figs. 2–11)

Vessel:	*Station*	*Occurrence*
Hugh M. Smith	144	2 females, 1.56, 1.60 mm.

Description: The head and first thoracic segment and fourth and fifth thoracic segments are separate (figs. 2, 3). The posterior lateral margins of the first thoracic segment are dis-

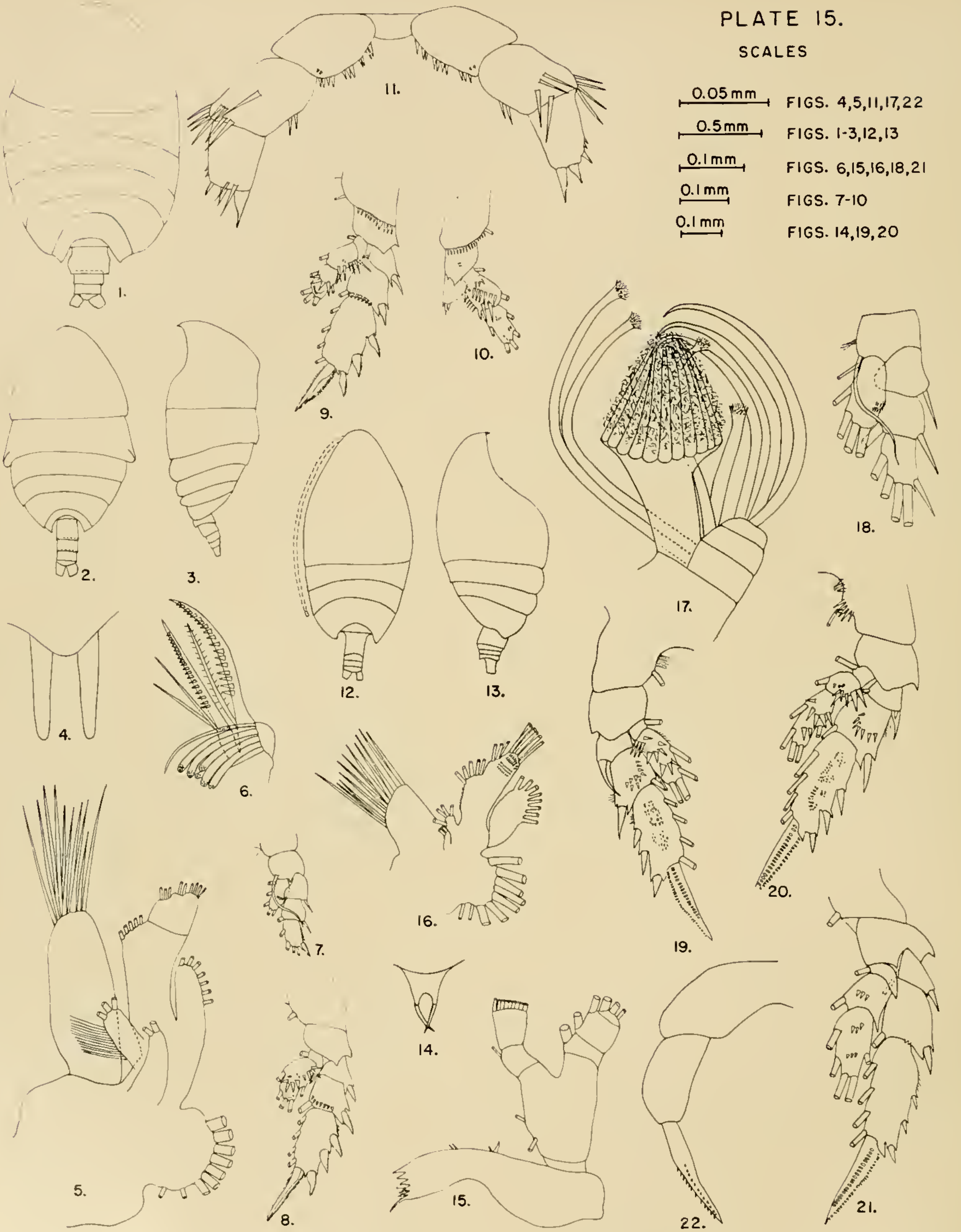

PLATE 15.—(1) *Phaenna spinifera*, female, dorsal view; (2) *Xanthocalanus dilatus* n.sp., female, dorsal view; (3) lateral view; (4) rostrum; (5) first maxilla, (6) terminal part of second maxilla; (7) first foot; (8) second foot; (9) third foot; (10) fourth foot (distal two segments of exopod missing); (11) fifth pair of feet (figs. 2–6 and 11 of holotype, figs. 7–10 of paratype); (12) *Amallophora smithae* n. sp., female, dorsal view; (13) lateral view; (14) rostrum; (15) mandible; (16) first maxilla; (17) terminal part of second maxilla; (18) first foot; (19) second foot; (20) third foot; (21) fourth foot; (22) fifth foot (figs. 12–22 of holotype).

tended and there is a distinct dilation on the dorsal surface of the head. The rostrum is straight and club-like (fig. 4).

The first antennae of both specimens are broken off near the proximal end. Although somewhat mutilated, the second antennae appear to have 1 seta on the first segment of the endopod. The second segment of the endopod has 14 setae on the distal margin (8 on the inner lobe and 6 on the outer lobe). The exopod has a total of 6 setae but some may be missing from the various segments.

The mandible has 3 setae on the basipod, 11 setae on the endopod and 6 on the exopod.

The first maxilla (fig. 5) has the following number of setae: 9 on the external lobe, 7 on the exopod, 9 on the endopod, 5 on the second basal segment, 2 on the second internal lobe and 3 on the third internal lobe.

The terminal part of the second maxilla (fig. 6) has 6 sensory organs and 1 worm-like appendage.

The exopods of the first 4 pairs of feet are 3-segmented (figs. 7–10), although the second and third exopodal segments of the fourth pair are broken off. The endopod of the first foot consists of 1 segment, of the second foot of 2 segments and of the third and fourth feet of 3 segments. The endopodal segments of the second and third feet have numerous spines arising from their posterior surfaces. A row of spines is present at the junction of the first and second basipodal segments, on the posterior side, of the third and fourth feet. The fifth foot (fig. 11) consists of 3 segments, all of which are furnished with either marginal or surface spines.

Remarks: This species differs from other described *Xanthocalanus* in (1) the dilations of the dorsal surface of the head and lateral margins of the first thoracic segment, (2) the spines on the basipodal segments of the third and fourth feet, and (3) the details of the fifth pair of feet. The fifth pair of feet closely resemble those of *X. agilis* Giesbrecht but *agilis* lacks the characteristic dilations of the head and first thoracic segment of the present species. In addition, *X. agilis* is a larger species (2.40 mm.). The presence of spines on the basipodal segments may also be found in other species of *Xanthocalanus*. Figures of these segments are available for only a few species.

The name proposed for this species is derived from the Latin word "dilato" and refers to the characteristic protrusions on the head and first thoracic segment. The holotype (U.S.N.M. No. 104, 420) and 1 paratype (No. 104, 421) have been deposited in the U.S. National Museum.

Amallophora smithae n. sp.

(PLATE 15, FIGS. 12–22)

Vessel:	*Station*	*Occurrence*
Hugh M. Smith	144	1 female, 1.40 mm.

Description: The head and first thoracic segments and the fourth and fifth thoracic segments are fused (fig. 12). In lateral view the posterior margin of the cephalothorax has a small indentation (fig. 13).

The first antennae are short and do not reach the end of the cephalothorax. Each antenna consists of 23 segments.

The endopod of the second antenna is slightly less than three-fourths the length of the exopod. Endopodal segment 1 has 2 setae. Segment 2 has 8 setae on the inner lobe and 7 setae on the outer lobe. The exopod has 8 setae all of which are densely plumose.

The basal segment of the mandibular palpus has 2 setae (fig. 15). There are 9 setae on the distal segment of the endopod and 1 seta on the proximal segment. The exopod has a total of 6 setae.

The first maxilla (fig. 16) has the following number of setae: 11 on the first inner lobe, 2 on the second inner lobe, 4 on the third inner lobe, 5 on the second basal segment, 9 on the endopod, 8 on the exopod and 9 on the external lobe. Two groups of small spines are present on the surface of the endopod.

The terminal part of the second maxilla (fig. 17) has 1 enlarged sensory organ, 4 smaller sensory organs and 3 worm-like appendages.

The first and second basal segments of the maxilliped have 7 and 5 setae, respectively. The 5 endopodal segments have the following number of setae: 4, 4, 3, 3 (plus 1 external seta), and 4.

The first pair of feet have 3-segmented exopods and 1-segmented endopods (fig. 18). The second pair of feet have exopods composed of 3 segments and endopods of 2 segments while the succeeding 2 pairs of feet each have 3-segmented exopods and endopods (figs. 19–21). The terminal spine of the second, third, and fourth pair of feet is characterized by an outer serrate margin and an inner row of small perforations. The endopods of the second and third feet have large spines arising from their surfaces. Numerous smaller spines are present on the 2 distal exopodal segments of the second and third feet. The fourth feet have a reduced number of spines.

The fifth feet (fig. 22) are small and consist of 2 segments. There is a stout and finely toothed spine arising from the distal segment.

Remarks: This species is closely related to *A. vorax* (Esterly, 1911). It differs from Esterly's species in the segmentation of the cephalothorax, cephalothorax-abdomen ratio, and the structure of the fifth feet. The fourth and fifth thoracic segments are separate in *A. vorax* but fused in *A. smithae.* Davis (1949) also reported that these segments in his specimen of *A. vorax* were fused. The cephalothorax is 6½ times longer than the abdomen in *A. vorax* according to Esterly; in the present species it is approximately 4 times the length of the abdomen. Davis stated that the abdomen of his specimen was longer than that reported by Esterly. In *A. vorax* there are two spines on the distal segment of the fifth feet. In *A. smithae* there is one robust spine.

Vervoort (1957) has discussed the genus *Amallophora* and pointed out differences between it and the genus *Xanthocalanus.* The structures of the maxillae and fifth feet appear to exclude the present species from the genus *Xanthocalanus* although the articulated rostral filaments are unlike those found in *Amallophora.* If Brodsky (1950) is correct in assigning Esterly's species (described as *Scolecithrix vorax*) to the genus *Amallothrix* then perhaps the present species should also be placed in this genus. Until the *Xanthocalanus–Amallothrix–Amallophora* complex is revised, I am referring the present species to the genus *Amallophora.*

The species is named for the research vessel *Hugh M. Smith.* The holotype is deposited in the U.S. National Museum (No. 104, 422).

Family SCOLECITHRICIDAE

Scolecithrix danae (Lubbock, 1856)

Pacific records: Esterly, 1905; Scott, 1909; Farran, 1929; Yamada, 1933; Farran, 1936; Mori, 1937; Dakin and Colefax, 1940; Johnson, 1942; Mori, 1942; Wilson, 1942; 1950; Anraku, 1952; Honjo, 1952; Nakai, 1952; Tanaka, 1953; Anraku, 1954b; Johnson, 1954; Tsuruta and Chiba, 1954b; Chiba, Tsuruta, and Maéda, 1955; Hida and King, 1955; Motoda and Anraku, 1955; Nagaya et al., 1955; Chiba, 1956; Honjo et al., 1957; Heinrich, 1958a; Yamazi, 1958a.

Vessel:	*Station*	*Occurrence*
Hugh M. Smith	132	present.
Do	144	present.
Do	153	present.
Do	178	present.
Do	30	present.
Do	31	3 females, 2.04–2.14 mm.
Do	29	3 females, 2.01–2.04 mm.
Do	63	4 females, 2.04–2.14; 3 males, 2.07–2.21 mm.
Stranger	34	2 females, 2.00, 2.04 mm.
Orsom	10	2 females, 2.01, 2.11; 1 male, 1.97 mm.
Horizon	32	3 females, 2.04; 2 males, 2.04, 2.11 mm.
Satsuma	32	2 females, 1.90, 2.00 mm.

Remarks: The posteriorly directed ventral protrusion on the female genital segment and the structure of the fifth feet of the male serve to identify this species. Figures of both these characters are given in Rose, 1933.

Scolecithrix bradyi Giesbrecht, 1888

(PLATE 16, FIGS. 1–5)

Pacific records: Esterly, 1905; Farran, 1929; 1936. As *Scolecithricella bradyi;* Scott, 1909; Mori, 1937; 1942; Wilson, 1942; 1950; Honjo, 1952; Tanaka, 1953; Chiba, Tsuruta, and Maéda, 1955; Motoda and Anraku, 1955; Nagaya et al., 1955; Chiba, 1956; Honjo et al., 1957.

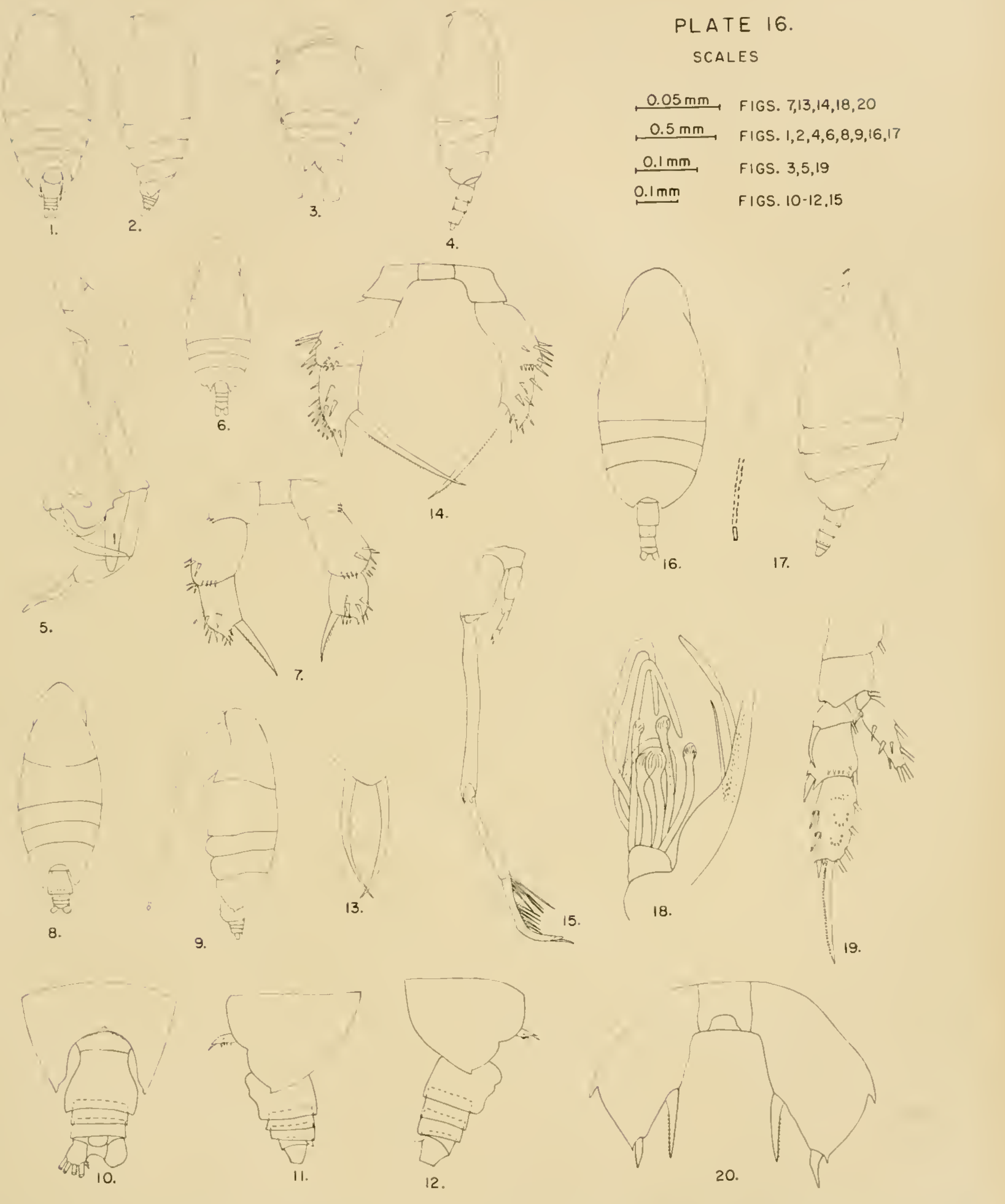

PLATE 16.—(1) *Scolecithrix bradyi*, female, dorsal view; (2) lateral view; (3) posterior part of thorax and abdomen, ventral view; (4) male, lateral view; (5) fifth pair of feet; (6) *Scolecithricella ctenopus*, female, juvenile, dorsal view; (7) fifth pair of feet; (8) adult, dorsal view; (9) lateral view; (10) posterior part of thorax and abdomen, dorsal view; (11) left side; (12) right side; (13) rostrum; (14) fifth pair of feet; (15) male, fifth pair of feet; (16) *S. abyssalis*, female, dorsal view; (17) lateral view; (18) terminal part of second maxilla; (19) second foot; (20) fifth pair of feet.

Vessel:	*Station*	*Occurrence*
Hugh M. Smith	94	11 females, 1.36–1.41; 2 males, 1.51, 1.56 mm.
Do	132	4 females, 1.33–1.36 mm.
Do	144	present.
Do	178	present.
Do	31	present.

Remarks: The asymmetrical posterior thoracic margins, the right one of which extends beyond the genital segment (fig. 1), serve to identify the female of this species. The male is recognized by the structure of the fifth feet (fig. 5).

Scolecithricella ctenopus (Giesbrecht, 1888)

(Plate 16, figs. 6–15)

Synonymy:

Scolecithrix ctenopus Giesbrecht, 1888, Atti Acc. Lincei Rend., ser. 4, 4 sem. 2: 338.

Scolecithricella ctenopus Sewell, 1929, Mem. Ind. Mus., 10: 212.

Scolecithrix longicornis T. Scott, 1894, Trans. Linn. Soc., Zool., 6: 50.

Scolecithricella spinipedata Mori, 1937, The pelagic Copepoda from the neighbouring waters of Japan, p. 53.

Pacific records: Scott, 1909; Farran, 1936; Tanaka, 1953.

Vessel:	*Station*	*Occurrence*
Hugh M. Smith	94	1 juvenile female, 1.28 mm.
Do	178	2 females, 1.49, 1.53; 1 male, 1.54 mm.
Stranger	34	1 female, 1.46; 1 male, 1.46 mm.
Orsom	10	1 female, 1.48 mm.

Remarks: Farran (1936) found two females which differed in size, segmentation of thorax and structure of fifth feet. He also reviewed the records and descriptions of *S. longicornis* (Scott, 1894) and considered it a synonym of *S. ctenopus*.

The present female specimens also fall into two size groups, the smaller of which is very similar to Farran's small specimen. The head and thorax in this form are separated by a fine line (in Farran's specimen they were fused) and a faint line is also seen to separate the fourth and fifth thoracic segments (fig. 6). Although the fifth feet are fairly well differentiated, the genital segment is undeveloped in this small specimen. In the larger form (figs. 8–14) the head and first thoracic segment are incompletely fused and the fourth and fifth thoracic segments are completely fused. The genital segment is well developed as are the fifth feet.

Although it is slightly larger, Mori's *S. spinipedata*, is, in my opinion, a synonym of *S. ctenopus*.

Scolecithricella abyssalis (Giesbrecht, 1888)

(Plate 16, figs. 16–20)

Pacific records: Scott, 1909; Mori, 1937; Tanaka, 1937; Wilson, 1942; 1950; Anraku, 1952; Tanaka, 1953; Brodsky, 1955; Chiba, Tsuruta, and Maéda, 1955; Nagaya et al., 1955; Chiba, 1956.

Vessel:	*Station*	*Occurrence*
Hugh M. Smith	94	6 females, 1.87–1.90 mm.
Do	144	1 female, 1.74 mm.
Do	29	1 female, 2.21 mm.
Do	63	1 female, 1.87 mm.

Remarks: Some variation was noted in the structure of the fifth feet of this species. Several specimens did not have the small spine-like protrusion near the terminal spine as shown in the fifth feet figured here (fig. 20).

Scolecithricella vittata (Giesbrecht, 1892)

(Plate 17, figs. 1–8)

Pacific records: Farran, 1936; Wilson, 1950; Tanaka, 1953.

Vessel:	*Station*	*Occurrence*
Hugh M. Smith	94	2 females, 1.66 mm.

Remarks: As in the preceding species, variation was noted in the fifth feet of this species. The terminal seta in one specimen was approximately twice the length of the proximal one (fig. 8) while in the other specimen it was somewhat shorter (fig. 4).

Scolecithricella tenuiserrata (Giesbrecht, 1892)

(Plate 17, figs. 9–21; plate 18, fig. 1)

Pacific records: Farran, 1936; Tanaka, 1953.

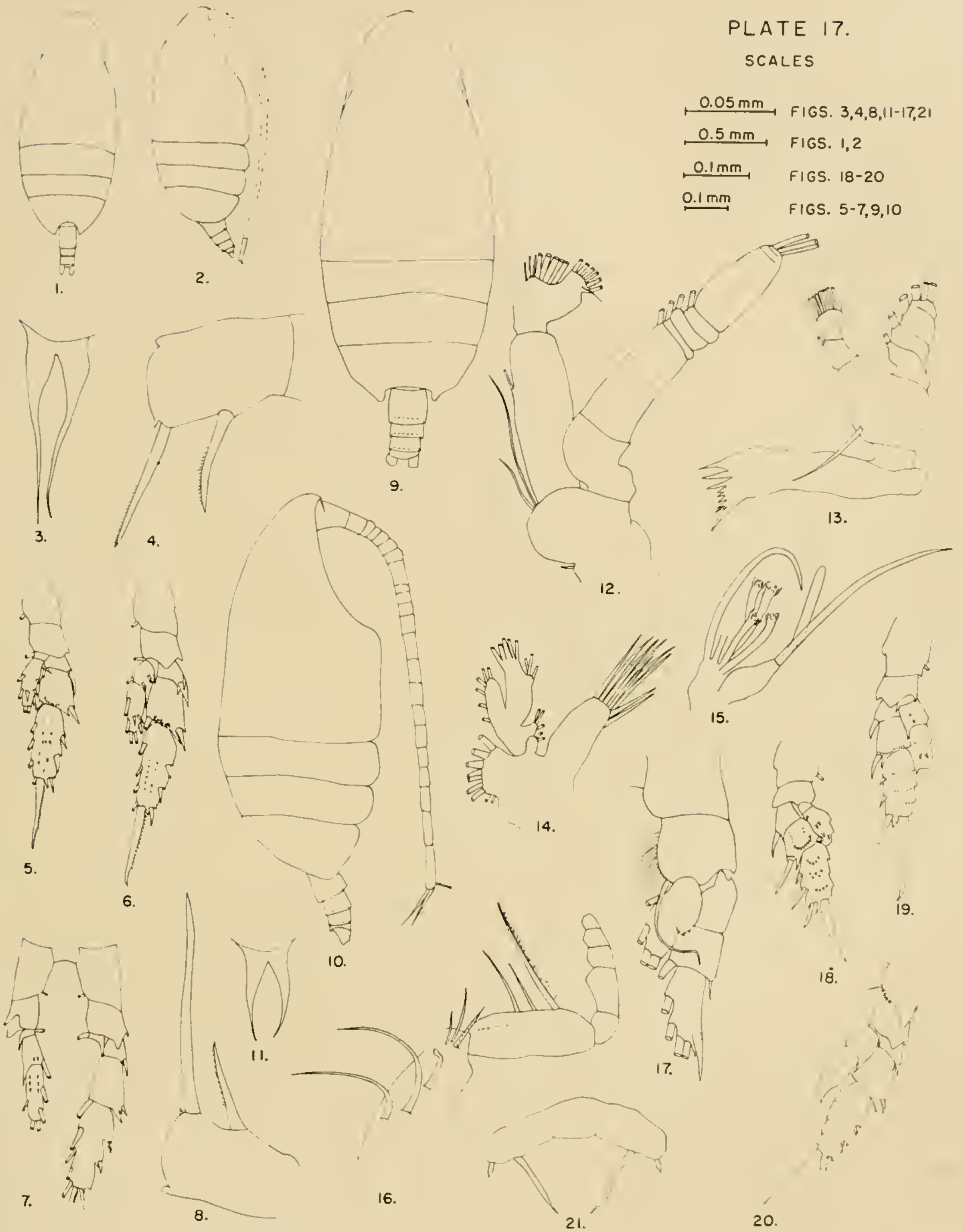

PLATE 17.—(1) *Scolecithricella vittata*, female, dorsal view; (2) lateral view; (3) rostrum; (4) fifth foot; (5) second foot; (6) third foot; (7) fourth pair of feet (one exopod and one endopod missing); (8) fifth foot; (9) *S. tenuiserrata*, female, dorsal view; (10) lateral view; (11) rostrum; (12) second antenna; (13) mandible; (14) first maxilla; (15) terminal part of second maxilla; (16) maxilliped (setae on endopod not shown); (17) first foot; (18) second foot (setae not shown); (19) third foot (setae not shown); (20) fourth foot (setae not shown); (21) fifth pair of feet.

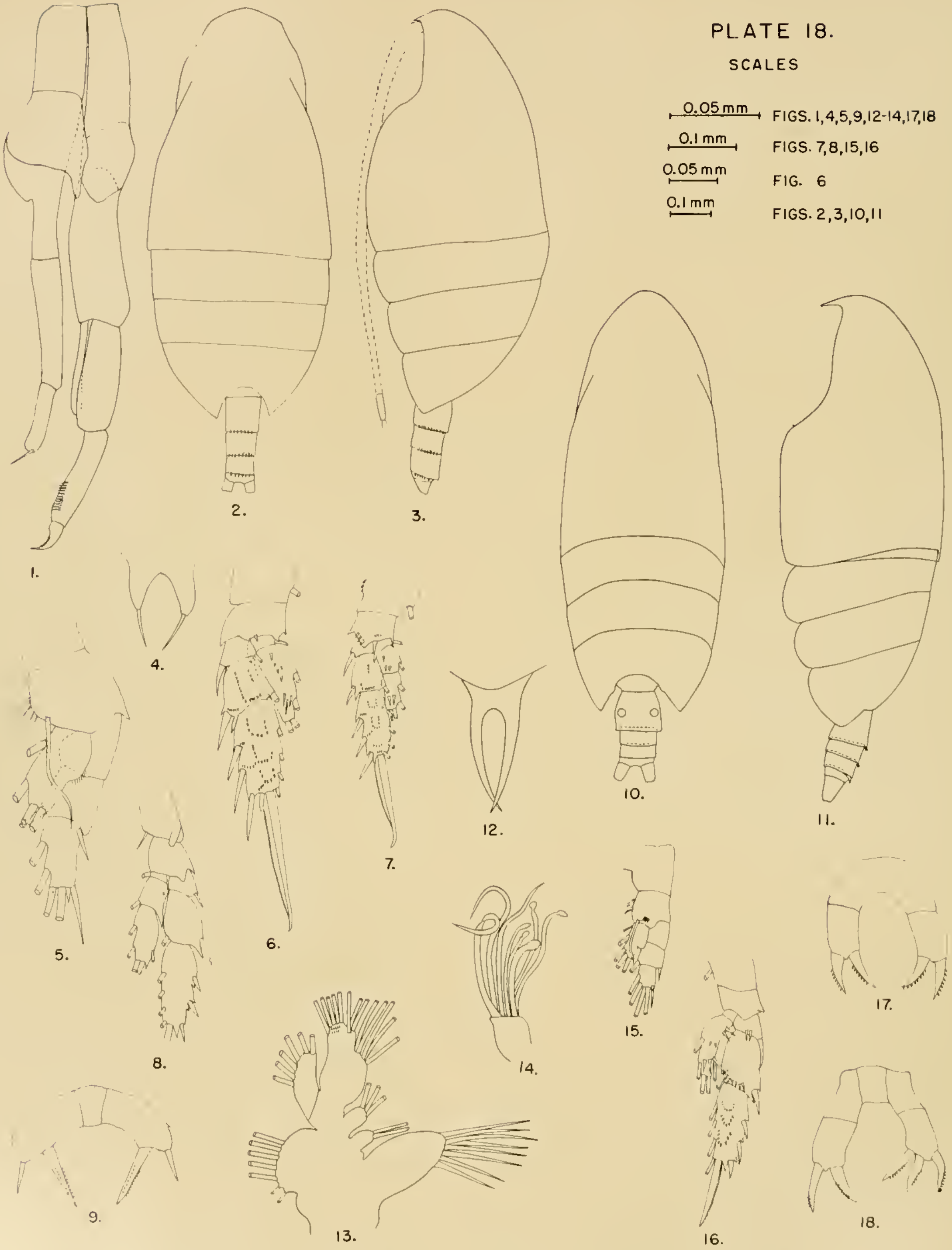

Plate 18.—(1) *Scolecithricella tenuiserrata*, male, fifth pair of feet; (2) *S. marginata*, female, dorsal view; (3) lateral view; (4) rostrum; (5) first foot; (6) second foot; (7) third foot; (8) fourth foot; (9) fifth pair of feet; (10) *Scolecithricella tropica* n. sp., female, dorsal view; (11) lateral view; (12) rostrum; (13) first maxilla; (14) terminal part of second maxilla; (15) first foot; (16) second foot; (17) fifth pair of feet; (18) fifth pair of feet, abnormal (figs. 10–18 of paratype).

Vessel:	Station	Occurrence
Hugh M. Smith	144	1 female, 1.08 mm.; 1 male, 1.17 mm.
Do	178	4 females, 1.05–1.10 mm.; 4 males, 1.0–1.27 mm.
Do	31	present.
Stranger	34	3 females, 1.02–1.10 mm.

Remarks: Because of the difficulty encountered in identifying this species, I have included several figures of the female and a figure of the fifth feet of a specimen that I consider to be the male of this species. Giesbrecht and Schmeil (1898) stated that the second basal segment of the first maxilla of the female has 5 setae. The present specimens have 3 setae on this segment. Although these authors indicated that the male of this species is questionable, they gave the length as 1.45 mm. as compared to 1.15 mm. for the female. The present males are also larger than the females.

Scolecithricella marginata (Giesbrecht, 1888)

(Plate 18, figs. 2–9)

Pacific records: Scott, 1909; Wilson, 1942.

Vessel:	Station	Occurrence
Hugh M. Smith	144	2 females, 1.05 mm.
Do	178	2 females, 1.00, 1.02 mm.

Remarks: The small size and fifth feet (fig. 9) serve to identify this species.

Scolecithricella tropica n. sp.

(Plate 18, figs. 10–18)

Vessel:	Station	Occurrence
Hugh M. Smith	94	4 females, 1.22–1.30 mm.
Do	132	5 females, 1.15–1.27 mm.
Do	178	2 females, 1.13, 1.14 mm.

Description: Of the 11 specimens of this species examined, none was intact. The following description is based, therefore, on several specimens and even with these a discussion of certain appendages will not be possible.

The cephalothorax is considerably longer than the abdomen, the ratio of these two body parts is approximately 4.4: 1.0 (figs. 10, 11). The posterior thoracic border has a well-defined indentation at a point just anterior to the apex. The genital segment is longer than the combined lengths of the next 2 segments. The rostral filaments are long and apparently not articulated to the base (fig. 12).

The first maxilla (fig. 13) has the following number of setae: 2 on the second inner lobe, 3 on the third inner lobe, 5 on the second basal segment, 8 on the endopod, and 6 on the exopod.

The terminal portion of the second maxilla (fig. 14) has 5 sensory and 3 worm-like appendages.

The first pair of feet (fig. 15) has a 3-segmented exopod and 1-segmented endopod. A group of small spines is present on the second basal segment near the distal margin. The exopod of the second pair of feet consists of 3 segments and the endopod of 2 segments (fig. 16). Two spines are present on the surface of the first exopodal segment, a group of large and small spines on the second segment and three groups of spines on the third exopodal segment. Five large and 2 small spines are present on the second endopodal segment.

As in certain other species of *Scolecithricella*, the fifth feet are variable. Most of the specimens examined have 2, approximately equal, terminal spines (fig. 17) but at least 2 specimens were observed to have 3 on one side and 2 on the other (fig. 18).

This species is distinguished from other species of *Scolecithricella* by the indentation on the posterior thoracic margin and the structure of the fifth feet.

Remarks: An undissected female from Station 94 was selected as the holotype (U.S.N.M. No. 104, 416). This specimen and 6 paratypes (Nos. 104, 417–104, 419) have been deposited in the U.S. National Museum.

Scolecithricella sp.

(Plate 19, figs. 1–5)

Vessel:	Station	Occurrence
Hugh M. Smith	144	2 males, 1.20, 1.22 mm.

Remarks: Two male specimens which are apparently referable to the genus *Scolecithri-*

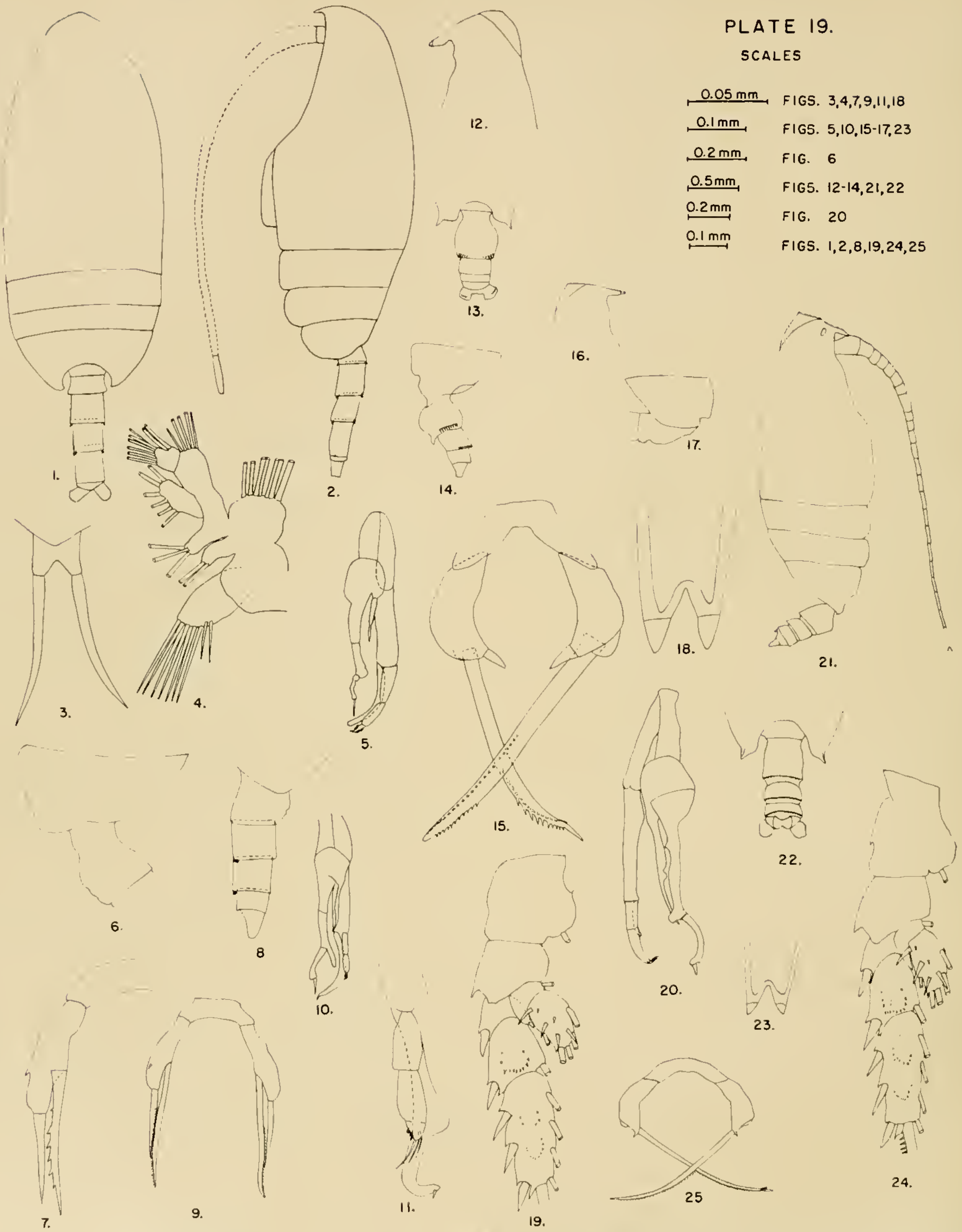

Plate 19.—(1) *Scolecithricella sp.*, male, dorsal view; (2) lateral view; (3) rostrum; (4) first maxilla; (5) fifth pair of feet; (6) *Scaphocalanus echinatus*, female, posterior part of thorax and genital segment; (7) fifth foot; (8) *S. longifurca*, female, posterior part of thorax and abdomen, lateral view; (9) fifth pair of feet; (10) male, fifth pair of feet; (11) left fifth foot; (12) *Scottocalanus securifrons*, female, forehead, lateral view; (13) abdomen, dorsal view; (14) posterior part of thorax and abdomen, lateral view; (15) fifth pair of feet; (16) *S. farrani*, male, forehead, lateral view; (17) posterior part of thorax and genital segment, lateral view; (18) rostrum; (19) second foot; (20) fifth pair of feet; (21) *S. sedatus*, female, lateral view; (22) abdomen, dorsal view; (23) rostrum; (24) second foot; (25) fifth pair of feet.

cella were found in the above sample. As the males of several described females, including the preceding species, are not known, I hesitate to describe the present species as new.

Scaphocalanus echinatus (Farran, 1905)

(PLATE 19, FIGS. 6, 7)

Pacific records: Farran, 1929, 1936; Mori, 1937; Wilson, 1950; Honjo, 1952; Tanaka, 1953; Tsuruta and Chiba, 1954a; Chiba, 1956; Honjo et al., 1957.

Vessel:	*Station*	*Occurrence*
Hugh M. Smith	63	1 female, 2.00 mm.

Remarks: *S. echinatus* resembles *S. longifurca* but the inner edge setae on the fifth feet of the former species are coarsely toothed (fig. 7).

Scaphocalanus longifurca (Giesbrecht, 1888)

(PLATE 19, FIGS. 8–11)

Pacific records: Tanaka, 1953. As *Scolecithricella longifurca*, Scott, 1909. As ?*Scaphocalanus gracilicauda*, Tanaka, 1937.

Vessel:	*Station*	*Occurrence*
Hugh M. Smith	94	1 male, 1.53 mm.
Do	29	2 females, 1.87, 1.94 mm.
Do	63	1 female, 1.94 mm.

Remarks: The similarity of this species to *S. subbrevicornis* has been pointed out by Farran (1929) and Vervoort (1951). The latter author has indicated that Tanaka's *S. gracilicauda* (male) is identical to a male doubtfully referred by Rose (1942) to *S. dentata*. Vervoort (1951) suggests that these two males may be the male of *S. longifurca*. I, too, have found a male specimen which I am tentatively referring to *S. longifurca* rather than to *S. subbrevicornis*, as figured by Vervoort, because of the small size of the present specimen (1.53). Vervoort's specimens measured 2.19 mm. and Tanaka's single specimen was 1.75 mm. The former author has also suggested (1957) that Wilson's (1950) records of *S. subbrevicornis* are probably referable to *S. longifurca*.

Scottocalanus securifrons (T. Scott, 1894)

(PLATE 19, FIGS. 12–15)

Pacific records: Scott, 1909; Farran, 1929; Tanaka, 1937; Brodsky, 1950; Wilson, 1950; Tanaka, 1953; Hida and King, 1955; Heinrich, 1958b.

Vessel:	*Station*	*Occurrence*
Horizon	32	1 female, 4.08 mm.

Remarks: The ventral surface of the genital segment is produced posteriorly and partly overlaps the following segment (fig. 14). The spine on the left fifth foot is thicker than that on the right (fig. 15). These two characters will identify the female of this species. No male has been found in the present samples.

Scottocalanus farrani A. Scott, 1909

(PLATE 19, FIGS. 16–20)

Pacific records: Scott, 1909; Wilson, 1950.

Vessel:	*Station*	*Occurrence*
Hugh M. Smith	29	1 male, 3.50 mm.

Remarks: The structure of the fifth pair of feet particularly the relative lengths of the exo- and endopods and the presence of a tooth-like process on the second basal segment of the right foot will identify the male of this species. No females were found.

Scottocalanus sedatus Farran, 1936

(PLATE 19, FIGS. 21–25)

Pacific records: Farran, 1936.

Vessel:	*Station*	*Occurrence*
Hugh M. Smith	29	1 female, 3.40 mm.
Orsom	10	1 female, 3.30 mm.

Remarks: This species is distinguished by the long setae and small, outwardly directed spines on the terminal segments of the fifth pair of feet (fig. 25).

Family TEMORIDAE

Temoropia mayumbaensis T. Scott, 1894

(PLATE 20, FIGS. 1–12)

Pacific records: Scott, 1909; Farran, 1929; 1936; Wilson, 1942; Heinrich, 1957b.

Vessel:	*Station*	*Occurrence*
Hugh M. Smith	94	6 females, 0.94–0.99; 3 males, 0.88–0.92 mm.
Orsom	10	2 females, 0.98 mm.

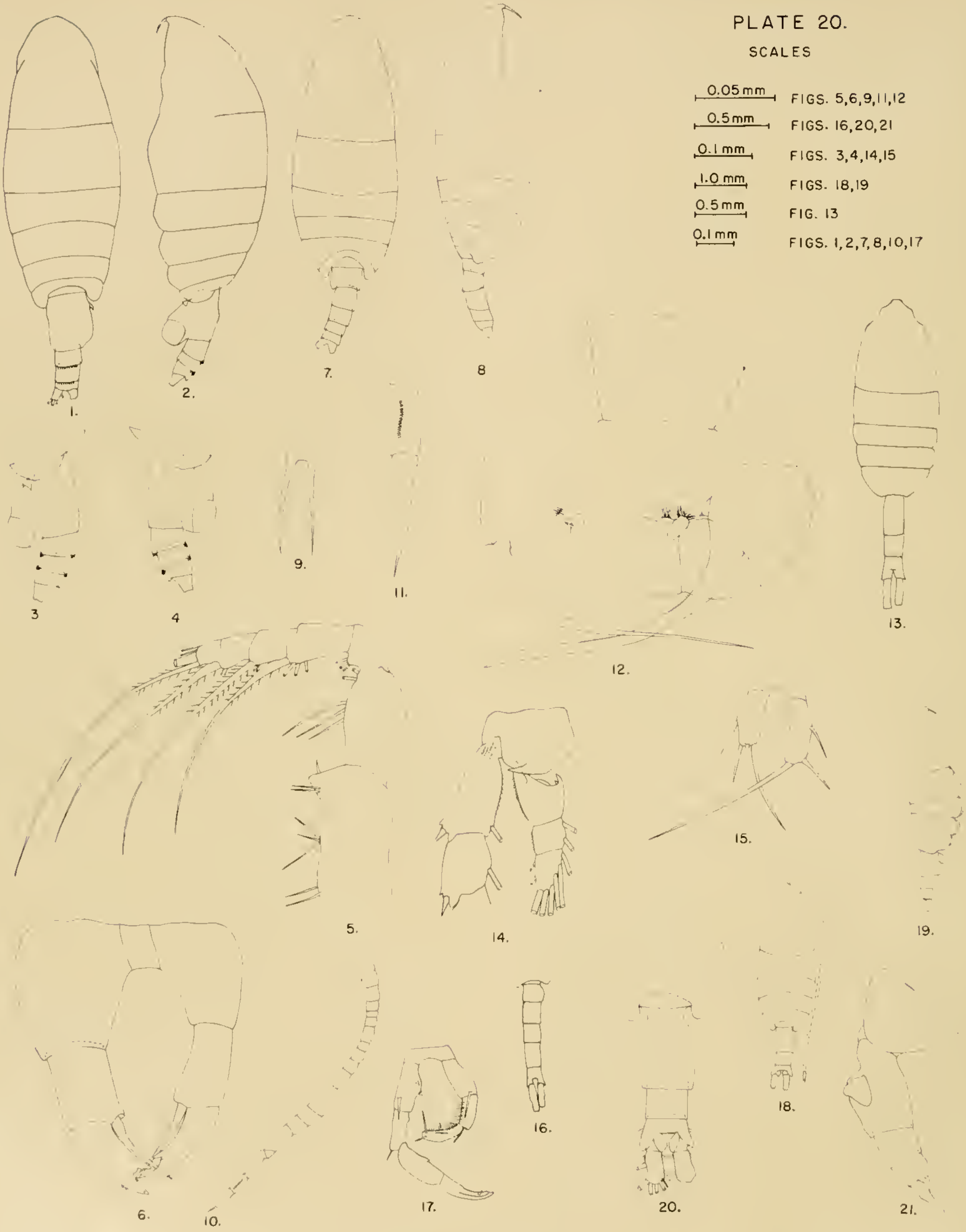

PLATE 20.—(1) *Temoropia mayumbaensis*, female, dorsal view; (2) lateral view; (3) posterior part of thorax and abdomen, left side; (4) posterior part of thorax and abdomen, right side; (5) maxilliped; (6) fifth pair of feet; (7) male, dorsal view; (8) lateral view; (9) rostrum; (10) first antenna; (11) distal two segments of first antenna; (12) fifth pair of feet; (13) *Metridia venusta*, female, dorsal view; (14) second foot (third exopodal segment omitted); (15) fifth pair of feet; (16) male, abdomen, dorsal view; (17) fifth pair of feet; (18) *Pleuromamma xiphias*, female, dorsal view; (19) lateral view; (20) posterior part of thorax and abdomen, dorsal view; (21) posterior part of thorax and abdomen, lateral view.

Remarks: The small size and large ventral protrusion on the genital segment (figs. 3, 4) will identify the female. The geniculate right antenna and the pointed terminal segment of this antenna (figs. 10, 11) will aid in recognizing the male sex.

Family METRIDIIDAE

Metridia venusta Giesbrecht, 1889

(Plate 20, figs. 13–17)

Pacific records: Vervoort, 1957.

Vessel:	Station	Occurrence
Hugh M. Smith	144	1 juvenile female, 2.88 mm.; 1 male, 2.82 mm.

Remarks: This species is recognized by the asymmetrical furca. In both sexes the left furca is longer than the right one (figs. 13, 16).

Vessel:	Station	Occurrence
Hugh M. Smith	63	1 male, 4.28 mm.
Orsom	10	2 females, 3.99, 4.08 mm.; 2 males, 3.99, 4.08 mm.
Satsuma	32	1 female, 4.25 mm.; 1 male, 4.18 mm.

Remarks: The large spine-like protrusion on the forehead of this species (figs. 19, 3) readily distinguishes it from other species in the genus.

Pleuromamma xiphias (Giesbrecht, 1888)

(Plate 20, figs. 18–21, plate 21, figs. 1–5)

Pacific records: Vervoort, 1957. Also, Johnson, 1942; Mori, 1942; Brodsky, 1950; Anraku, 1952; Honjo, 1952; Anraku, 1954b; Tsuruta and Chiba, 1954a; 1954b; Chiba, Tsuruta, and Maéda, 1955; Hida and King, 1955; Nagaya et al., 1955; Chiba, 1956; Heinrich, 1957b; Honjo et al., 1957; Heinrich, 1958b; Yamazi, 1958a.

Pleuromamma abdominalis (Lubbock, 1856)

(Plate 21, figs. 6–15)

Pacific records: Vervoort, 1957. Also, Johnson, 1942; Mori, 1942; Brodsky, 1950; Anraku, 1952; Honjo, 1952; Anraku, 1954a; 1954b; Tsuruta and Chiba, 1954b; Chiba, Tsuruta, and Maéda, 1955; Hida and King, 1955; Nagaya et al., 1955; Chiba, 1956; Heinrich, 1957b; Honjo et al., 1957; Heinrich, 1958a; Yamazi, 1958a.

Vessel:	Station	Occurrence (*measurements in mm.; number of specimens in paren.*)			
		f. *typica*		f. *edentata*	f. *abyssalis*
		female	male	female	male
Hugh M. Smith	94	3.02(2)			
Do	29		3.13(1)	2.75–3.06(11)	3.06(1)
Do	63			2.75–2.82(2)	
Orsom	10		2.79–3.02(3)		
Horizon	32	3.06(1)			
Satsuma	32	2.85–3.13(5)	2.99–3.06(4)		

Remarks: All three forms of this species appeared in the above cited samples. Figures and descriptions of these have been presented by Steuer (1932). The female of forma *abyssalis* is not known. The female of forma *typica* and forma *edentata* are distinguished by the teeth on the first and second antennal segments. In forma *typica* these segments each has a large tooth (fig. 6) while in forma *edentata* these segments have only small teeth (fig. 10). Although Steuer mentions that segment 16 of the first antenna is smaller than segment 17 in forma *edentata*, these length differences are difficult to observe.

The male of forma *edentata* is unknown. Forma *typica* is easily recognized by the greatly asymmetrical and hairy abdomen (fig. 7) while the male of forma *abyssalis* has a less asymmetrical and less hairy abdomen (fig. 12). The small tooth on segment 17 (fig. 13) makes this specimen referable to what Steuer termed subform *thermophila* of forma *abyssalis*.

Pleuromamma indica Wolfenden, 1905

(Plate 22, figs. 1–7)

Pacific records: Tanaka, 1953.

Vessel:	Station	Occurrence
Satsuma	32	1 male, 2.04 mm.

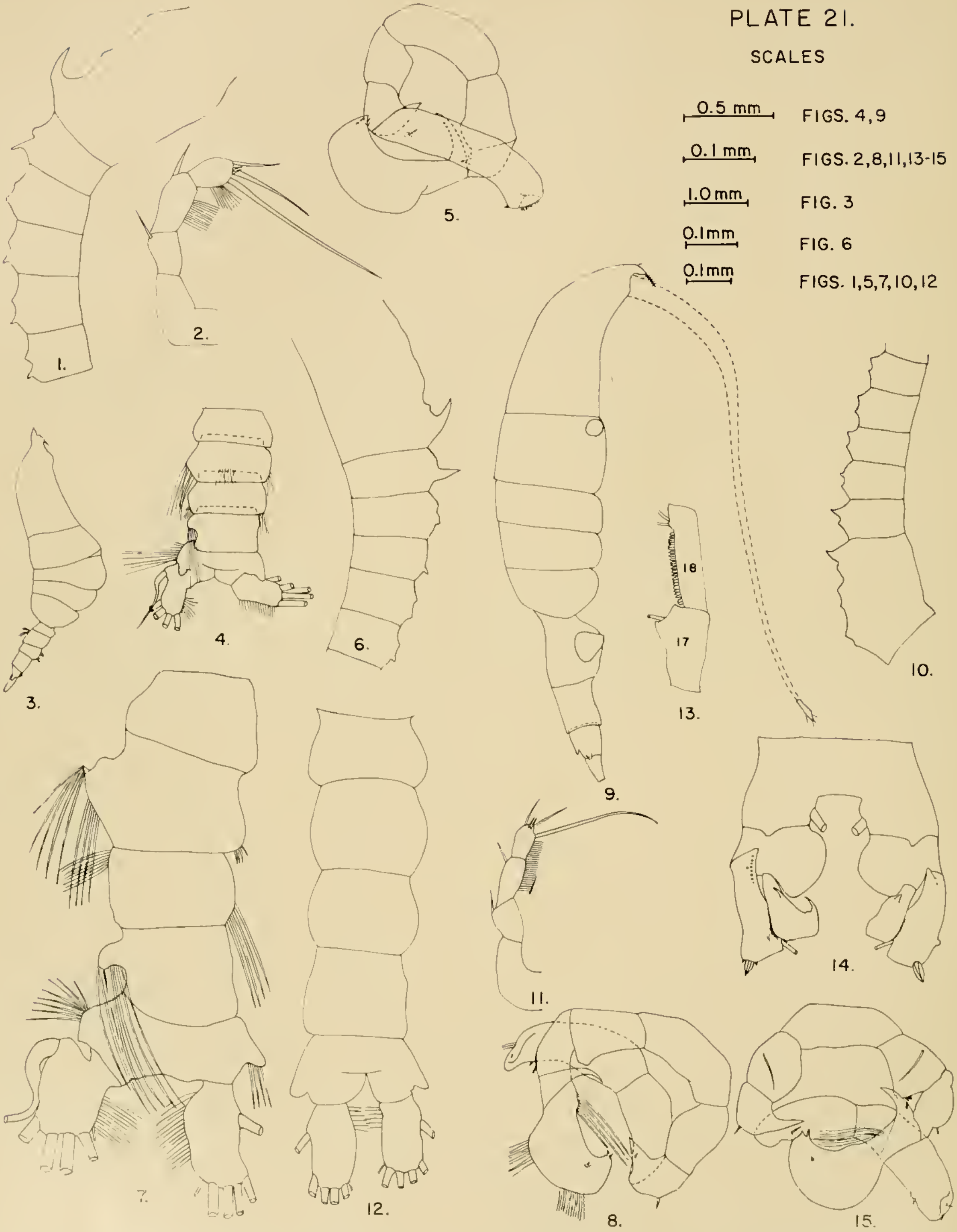

Plate 21.—(1) *Pleuromamma xiphias*, female, proximal part of first antenna; (2) fifth foot; (3) male, lateral view; (4) abdomen, dorsal view; (5) fifth pair of feet; (6) *P. abdominalis* f. *typica*, female, proximal part of first antenna; (7) male, abdomen, dorsal view; (8) fifth pair of feet; (9) *P. abdominalis* f. *edentata*, female, lateral view; (10) proximal part of first antenna; (11) fifth foot; (12) *P. abdominalis* f. *abyssalis*, male, abdomen, dorsal view; (13) segments 17 and 18 of right first antenna; (14) second pair of feet (distal end of exopods and endopods not shown); (15) fifth pair of feet.

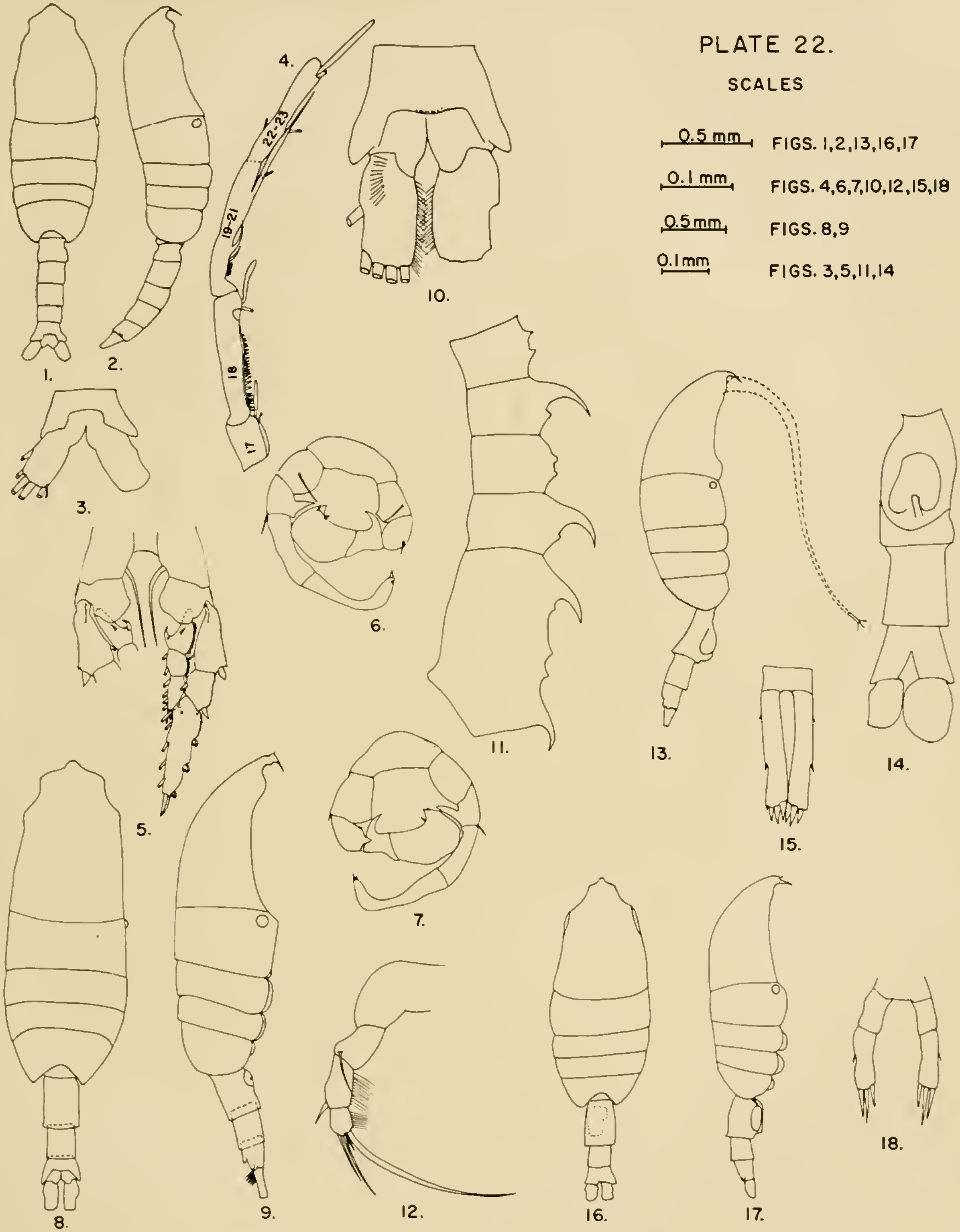

PLATE 22.—(1) *Pleuromamma indica*, male, dorsal view; (2) lateral view; (3) anal segment and furcae, dorsal view; (4) segments 17 to 23 of right first antenna; (5) second pair of feet (only part of one foot shown); (6) fifth pair of feet, anterior side; (7) posterior side; (8) *P. quadrungulata* f. *typica*, female, dorsal view; (9) lateral view; (10) anal segment and furcae, dorsal view; (11) proximal part of first antenna; (12) fifth foot; (13) *P. gracilis* f. *minima*, female, lateral view; (14) abdomen, ventral view; (15) fifth pair of feet; (16) *P. borealis*, female, dorsal view; (17) lateral view; (18) fifth pair of feet.

Remarks: Only a single male of this species was found. It is distinguished from males of *abdominalis* and other species by the symmetrical abdomen (fig. 1), divergent furcae (fig. 3) and absence of teeth on segment 17 of the right first antenna (fig. 4). The first segment of both endopods of *indica* are indented and claw-like (fig. 5) in contradistinction to *abdominalis* which has this claw-like indentation on only one endopod.

Pleuromamma quadrungulata (Dahl, 1893)

(Plate 22, figs. 8–12)

Pacific records: Vervoort, 1957. Also, Brodsky, 1950.

Vessel:	*Station*	*Occurrence*
Hugh M. Smith	29	1 female, 3.77 mm.
Do	63	1 female, 3.51 mm.

Remarks: The above specimens are referable to forma *typica* Steuer, 1932. It is distinguished from forma *psychrophila* Steuer, 1931, by the presence of a large curved tooth on the fourth segment of the first antennae (fig. 11). In forma *psychrophila* this tooth is reduced in size and not curved.

Pleuromamma gracilis (Claus, 1863)

(Plate 22, figs. 13–15)

Pacific records: Esterly, 1905; Scott, 1909; Farran, 1929; 1936; Mori, 1937; Tanaka, 1937; Dakin and Colefax, 1940; Johnson, 1942; Mori, 1942; Wilson, 1942; Brodsky, 1950; Wilson, 1950; Anraku, 1952; Honjo, 1952; Tanaka, 1953; Anraku, 1954b; Tsuruta and Chiba, 1954b; Chiba, Tsuruta, and Maéda, 1955; Nagaya et al., 1955; Chiba, 1956; Heinrich, 1957b; Honjo et al., 1957; Heinrich, 1958a; 1958b; Yamazi, 1958a.

Vessel:	*Station*	*Occurrence*
Hugh M. Smith	94	1 female, 1.80 mm.
Do	29	6 females, 2.01–2.07 mm.
Do	63	1 female, 1.90 mm.
Horizon	32	1 female, 1.94 mm.
Satsuma	32	1 female, 1.97 mm.

Remarks: All the specimens obtained of this species are referable to Steuer's (1932) forma *minima*. This form is distinguished from forma *piseki* (Farran, 1929) and *maxima* (Steuer, 1932) by the divergent margins of the anal segment (fig. 14) and by the fused second basal and exopodal segments of the fifth feet (fig. 15). In most of the present specimens the left furca is enlarged (fig. 14).

Pleuromamma borealis (Dahl, 1893)

(Plate 22, figs. 16–18)

Pacific records: Farran, 1929; Brodsky, 1950; Wilson, 1950.

Vessel:	*Station*	*Occurrence*
Hugh M. Smith	63	1 female, 2.01 mm.
Orsom	10	1 female, 1.83 mm.
Satsuma	32	2 females, 1.90 mm.

Remarks: The long spines on the fifth feet of the female (fig. 18) distinguished this species from the preceding one.

Family CENTROPAGIDAE

Centropages gracilis (Dana, 1849)

(Plate 23, figs. 1–3)

Pacific records: Scott, 1909; Yamada, 1933; Farran, 1936; Mori, 1937; Dakin and Colefax, 1940; Mori, 1942; Wilson, 1950; Tanaka, 1953; Tsuruta and Chiba, 1954b; Chiba, Tsuruta, and Maéda, 1955; Nagaya et al., 1955; Chiba, 1956; Honjo et al., 1957; Yamazi, 1958a.

Vessel:	*Station*	*Occurrence*
Hugh M. Smith	132	3 females, 1.90–1.97 mm.
Do	153	present.
Do	178	2 females, 2.00 mm.
Do	30	3 females, 1.97–2.01 mm.; 1 male, 2.04 mm.
Stranger	34	1 female, 1.90 mm.
Satsuma	32	1 male, 1.84 mm.

Remarks: The female is recognized by the spines on the sides on the second abdominal segment and the short spine-like protrusions on the inner sides of the second exopodal segments (fig. 1) of the fifth feet. The thumb of the chela of the right foot of the male has a

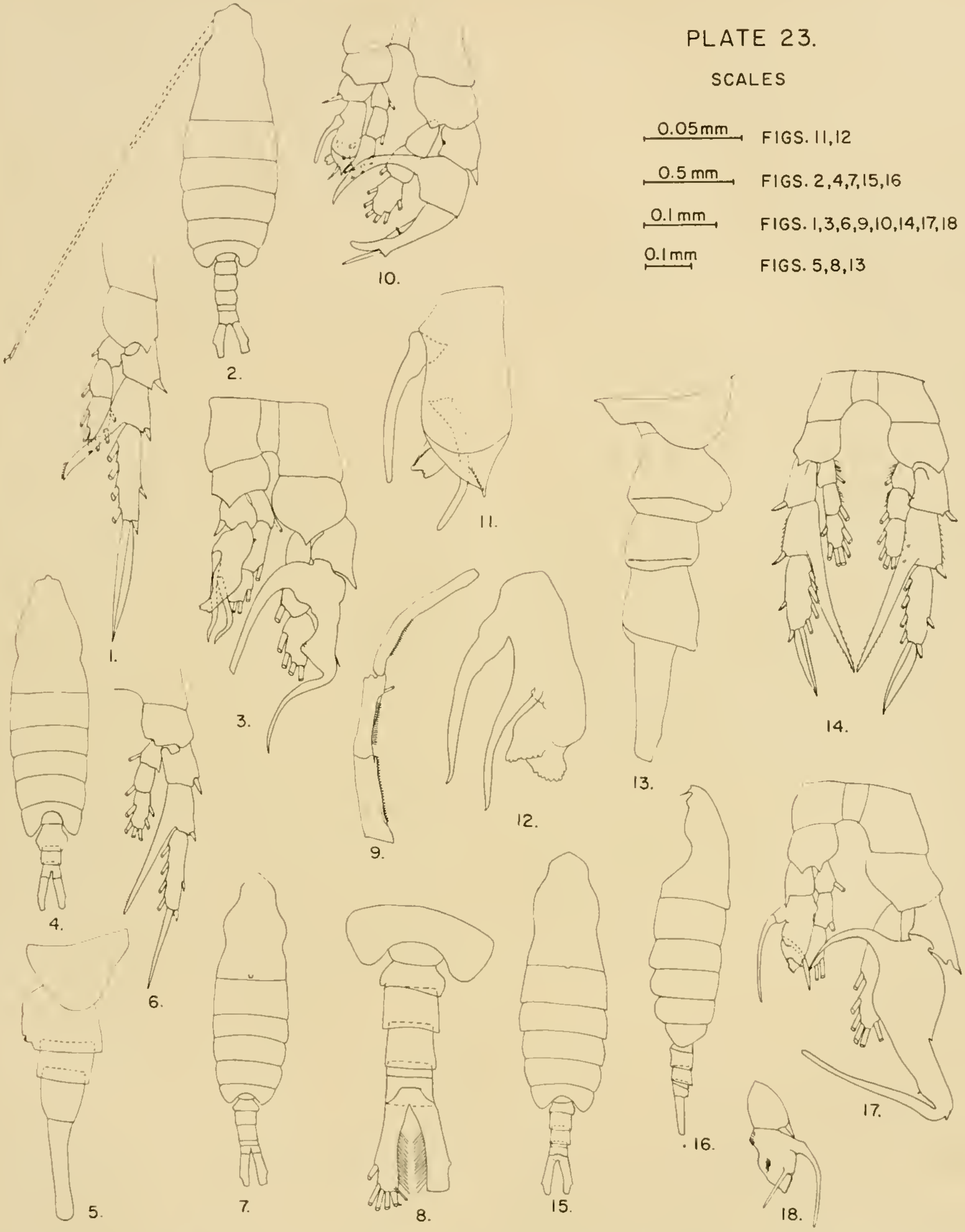

PLATE 23.—(1) *Centropages gracilis*, female, fifth foot; (2) male, dorsal view; (3) fifth pair of feet; (4) *C. elongatus*, female, dorsal view; (5) posterior part of thorax and abdomen, lateral view; (6) fifth foot; (7) male, dorsal view; (8) posterior part of thorax and abdomen, dorsal view; (9) segments 17 to 21 of right first antenna: (10) fifth pair of feet; (11) terminal part of exopod of left fifth foot; (12) terminal part of exopod of left fifth foot, other side; (13) *C. calaninus*, female, posterior part of thorax and abdomen, lateral view; (14) fifth pair of feet; (15) male, dorsal view; (16) lateral view; (17) fifth pair of feet; (18) exopod of left fifth foot.

pronounced triangular protrusion which is absent in other species in the genus (fig. 3).

Centropages elongatus Giesbrecht, 1896

(Plate 23, figs. 4–12)

Synonymy:

Centropages pacificus Chiba, 1956, Jour. Shimonoseki College of Fisheries, 6(1): 47–48.

Pacific records: Scott, 1909; Mori, 1937; 1942; Wilson, 1942; Johnson, 1954; Tsuruta and Chiba, 1954b; Chiba, Tsuruta, and Maéda, 1955; Nagaya et al., 1955; Yamazi, 1958a.

Vessel:	*Station*	*Occurrence*
Hugh M. Smith	153	1 female, 1.87 mm.
Horizon	32	2 males, 1.74, 1.76 mm.
Satsuma	32	1 female, 1.66 mm.

Remarks: The female genital segment is only slightly asymmetrical (figs. 4, 5) and the abdomen lacks the spines which are present in the preceding species and in a related species (*C. violaceus*). The spine-like extensions of the second exopodal segments of the fifth feet exceed the distal end of the third exopodal segments (fig. 6). The male is recognized by the structure of the fifth feet, particularly the long external spine near the distal end of the thumb (fig. 10) and the form of the left exopod (figs. 11, 12).

Chiba (1956) has described a new species, *C. pacificus* (based on males), from specimens collected in the Bikini area. I believe these specimens are the males of *C. elongatus*, a species which has also been reported from Bikini by Johnson (1954).

Mori (1937) stated in his discussion of this species that the last thoracic segments of the female are pointed. He also presented a figure showing this point on one lateral margin. However, no mention was made of the pointed margins of the last thoracic segments by Giesbrecht (1896) in his original description of the species nor in the synopsis of this species presented later by Giesbrecht and Schmeil (1898). The latter authors stated that *C. elongatus* is related to *C. violaceus* which has round posterior thoracic margins. The present specimens also have rounded margins (fig. 5).

Centropages calaninus (Dana, 1849)

(Plate 23, figs. 13–18)

Pacific records: Scott, 1909; Farran, 1936; Mori, 1937; Dakin and Colefax, 1940; Mori, 1942; Wilson, 1942; 1950; Tanaka, 1953; Tsuruta and Chiba, 1954b; Chiba, Tsuruta, and Maéda, 1955; Nagaya et al., 1955; Chiba, 1956; Gilmartin, 1958; Yamazi, 1958a.

Vessel:	*Station*	*Occurrence*
Hugh M. Smith	30	1 female, 2.18 mm.; 1 male, 2.06 mm.
Horizon	32	3 females, 1.97–2.04 mm.; 5 males, 1.80–2.00 mm.

Remarks: The anal segment of the female has a small knob on the ventral surface near the posterior end and the spine-like protrusions of the second exopodal segments of the fifth feet exceed the tip of the third exopodal segments (figs. 13, 14). The male is recognized by the structure of the fifth feet, especially the long and bent thumb of the chela (fig. 17).

Family LUCICUTIIDAE

Lucicutia flavicornis (Claus, 1863)

(Plate 24, figs. 1–4)

Pacific records: Esterly, 1905; Scott, 1909; Farran, 1929; Mori, 1937; Dakin and Colefax, 1940; Johnson, 1942; Mori, 1942; Wilson, 1942; Davis, 1949; Brodsky, 1950; Wilson, 1950; Anraku, 1952; Honjo, 1952; Tanaka, 1953; Anraku, 1954b; Tsuruta and Chiba, 1954b; Chiba, Tsuruta, and Maéda, 1955; Motoda and Anraku, 1955; Nagaya et al., 1955; Chiba, 1956; Heinrich, 1957b; Honjo et al., 1957; Heinrich, 1958a; Yamazi, 1958a.

Vessel:	*Station*	*Occurrence*
Hugh M. Smith	94	12 females, 1.46–1.90 mm.; 7 males, 1.43–1.77 mm.
Do	132	3 males, 1.29–1.66 mm.
Do	144	4 females, 1.63–1.80 mm.; 5 males, 1.44–1.48 mm.
Do	178	3 females, 1.36–1.53 mm.; 7 males, 1.28–1.42 mm.

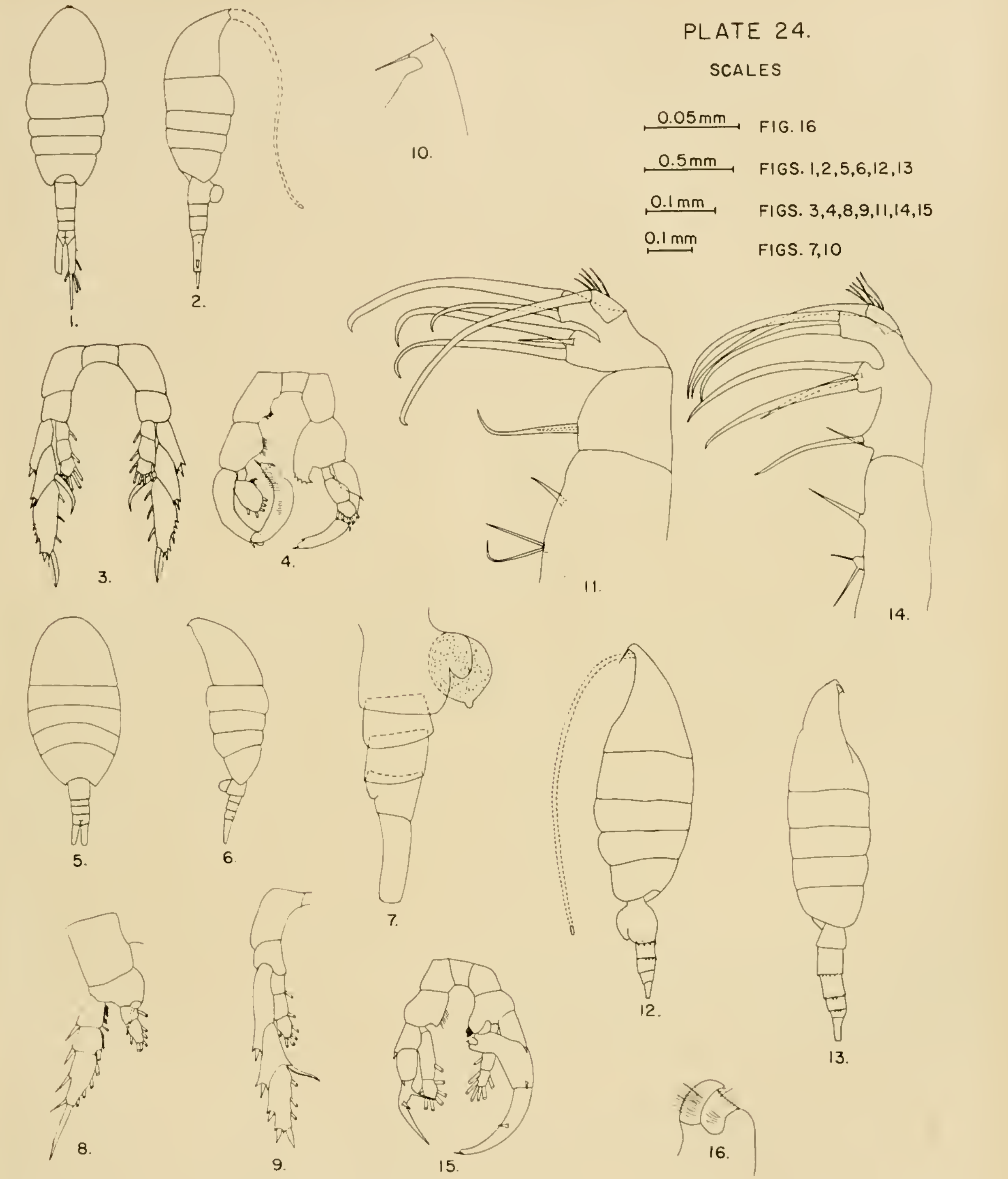

Plate 24.—(1) *Lucicutia flavicornis*, female, dorsal view; (2) lateral view; (3) fifth pair of feet; (4) male, fifth pair of feet; (5) *L. ovalis*, female, dorsal view; (6) lateral view; (7) abdomen, lateral view; (8) first foot; (9) fifth foot; (10) *Heterorhabdus spinifrons*, female, forehead, lateral view; (11) second maxilla; (12) *H. papilliger*, female, lateral view; (13) male, lateral view; (14) second maxilla; (15) fifth pair of feet; (16) distal end of protrusion of second right exopodal segment.

Vessel:	*Station*	*Occurrence*
Do	31	3 females, 1.41–1.55 mm.
Do	29	present.
Stranger	34	1 female, 1.39 mm.
Satsuma	32	1 female, 1.26 mm.

Remarks: The female is distinguished from other species of the genus by the short anal segment (figs. 1, 2) and by the form of the fifth feet (fig. 3). The male is recognized by the protrusion of the second basipodal segment of the left foot and the long terminal segment of the right exopod (fig. 4).

Other authors, including Farran, 1929, mention that considerable variation occurs in the length of this species. In at least one collection (*Smith* 94), two size groups were noted as follows: females 1.46–1.53 (6); 1.87–1.90 (6); males 1.39–1.53 (7); 1.77 (1) mm.

Lucicutia ovalis Wolfenden, 1911

(Plate 24, figs. 5–9)

Pacific records: Farran, 1929; 1936; Mori, 1937; Wilson, 1950; Tanaka, 1953; Anraku, 1954b; Tsuruta and Chiba, 1954b; Chiba, Tsuruta, and Maéda, 1955; Motoda and Anraku, 1955; Nagaya et al., 1955; Chiba, 1956; Honjo et al., 1957; Yamazi, 1958a.

Vessel:	*Station*	*Occurrence*
Hugh M. Smith	132	2 females, 1.32, 1.36 mm.
Do	153	1 female, 1.37 mm.
Do	178	3 females, 1.34–1.36 mm.
Do	63	1 female, 1.46 mm.
Stranger	34	1 female, 1.39 mm.
Orsom	10	present.
Satsuma	32	1 female, 1.44 mm.

Remarks: The female is most easily recognized by its small size, the two-segmented endopod of the first feet (fig. 8), and the structure of the fifth feet (fig. 9).

Family HETERORHABDIDAE

Heterorhabdus spinifrons (Claus, 1863)

(Plate 24, figs. 10–11)

Pacific records: Vervoort, 1957. Also, Brodsky, 1950; Tanaka, 1953.

Vessel:	*Station*	*Occurrence*
Hugh M. Smith	144	present.
Do	29	3 females, 2.69–3.57 mm.; 3 males, 3.04–3.20 mm.
Do	63	1 male, 2.41 mm.
Satsuma	32	3 females, 2.10–2.18 mm.

Remarks: In both sexes the forehead is prolonged into a point (fig. 10), a character which will identify this species. In the female, one of the distal 3 spines of the maxilliped is small and slender (fig. 11).

Heterorhabdus papilliger (Claus, 1863)

(Plate 24, figs. 12–16)

Pacific records: Esterly, 1905; Scott, 1909; Farran, 1929; 1936; Mori, 1937; Tanaka, 1937; Dakin and Colefax, 1940; Johnson, 1942; Mori, 1942; Wilson, 1942; Brodsky, 1950 Wilson, 1950; Anraku, 1952; Honjo, 1952; Tanaka, 1953; Anraku, 1954a; 1954b; 1954c; Chiba, Tsuruta, and Maéda, 1955; Motoda and Anraku, 1955; Nagaya et al., 1955; Chiba, 1956; Heinrich, 1957b; Yamazi 1958a.

Vessel:	*Station*	*Occurrence*
Hugh M. Smith	94	2 females, 2.04, 2.07 mm.; 3 males, 1.80–1.94 mm.
Do	132	2 females, 1.87, 1.90 mm.; 1 male, 1.87 mm.
Do	144	1 female, 2.14 mm.; 1 male, 2.11 mm.
Do	178	6 females, 1.80–1.87 mm.; 6 males, 1.70–1.84 mm.
Do	29	1 female, 2.00 mm.
Do	31	4 females, 1.90–1.94 mm.; 1 male, 1.97 mm.
Do	63	2 females, 1.77, 1.97 mm.
Stranger	34	1 female, 1.94 mm.
Orsom	10	1 female, 1.84 mm.

Remarks: The female forehead is rounded (fig. 12) and the 3 distal spines of the maxilliped are all about equal in length in both sexes (fig. 14).

Family AUGAPTILIDAE

Haloptilus acutifrons (Giesbrecht, 1892)

(Plate 25, figs. 1–8)

Pacific records: Vervoort, 1957. Also, Johnson, 1942; Brodsky, 1950; Tanaka, 1953; Anraku, 1954b; Chiba, Tsuruta, and Maéda, 1955; Nagaya et al., 1955; Chiba, 1956; Yamazi, 1958a.

Vessel:	*Station*	*Occurrence*
Hugh M. Smith	94	1 female, 3.80 mm.

Remarks: Although closely resembling *H. oxycephalus*, *H. acutifrons* may be distinguished by (1) its small size, (2) less produced forehead (fig. 1) and (3) structure of the gnathal lobe of the mandible (fig. 3).

Haloptilus fertilis (*Giesbrecht*, 1892)

(Plate 25, figs. 9–11)

Pacific records: none.

Vessel:	*Station*	*Occurrence*
Hugh M. Smith	32	1 male, 2.47 mm.

Remarks: The male is recognized by its small size and structure of the fifth feet (fig. 11).

Haloptilus longicornis (Claus, 1863)

Pacific records: Scott, 1909; Farran, 1929; 1936; Mori, 1937; Johnson, 1942; Mori, 1942; Wilson, 1942; Brodsky, 1950; Wilson, 1950; Tanaka, 1953; Yamazi, 1953c; Chiba, Tsuruta, and Maéda, 1955; Nagaya et al., 1955; Chiba, 1956; Heinrich, 1957b; Honjo et al., 1957; Heinrich, 1958b; Yamazi, 1958a.

Vessel:	*Station*	*Occurrence*
Hugh M. Smith	94	present.
Do	132	9 females, 1.80–1.90 mm.
Do	144	present.
Do	153	Do
Do	178	Do
Do	31	Do
Do	63	Do
Stranger	34	Do
Orsom	10	Do
Horizon	32	Do
Satsuma	32	5 females, 1.77–1.83 mm.

Remarks: The long first antennae which exceed the end of the furca and the knob-like button on the forehead will identify the female. No males were found.

As the occurrence records indicate, this was a widespread species in the present collections. It was also the most abundant species of *Haloptilus* and occurred in fair numbers in several samples (*Smith* 94, 144, 31).

Haloptilus ornatus (Giesbrecht, 1892)

(Plate 25, figs. 12–16)

Pacific records: Scott, 1909; Mori, 1937; Johnson, 1942; Wilson, 1942; Wilson, 1950; Tanaka, 1953; Anraku, 1954b; Chiba, Tsuruta, and Maéda, 1955; Nagaya et al., 1955; Chiba, 1956.

Vessel:	*Station*	*Occurrence*
Hugh M. Smith	63	1 female, 4.56 mm.

Remarks: This is a large species and has a rounded forehead. As in other species of *Haloptilus*, the form of the gnathal lobe of the mandible is also diagnostic (fig. 13).

Haloptilus spiniceps (Giesbrecht, 1892)

(Plate 25, figs. 17–20; plate 26, figs. 1–5)

Pacific records: Scott, 1909; Farran, 1929; 1936; Mori, 1937; Dakin and Colefax, 1940; Johnson, 1942; Wilson, 1942; 1950; Tanaka, 1953.

Vessel:	*Station*	*Occurrence*
Hugh M. Smith	94	1 female, 3.99 mm.
Stranger	34	1 female, 3.70 mm.
Orsom	10	present.
Horizon	32	1 female, 3.80 mm.
Satsuma	32	1 female, 3.80 mm.

Remarks: The short pointed forehead (fig. 17) which is curved downward in lateral view (fig. 18) and the structure of the gnathal lobe of the mandible (fig. 20) will identify the female of this species. No male has been found.

Haloptilus austini Grice, 1959

Pacific records: Grice, 1959.

Vessel:	*Station*	*Occurrence*
Hugh M. Smith	94	2 females, 3.16, 3.33 mm.

Remarks: I have recently described this species. It has a rounded forehead and, as in other species of *Haloptilus*, the gnathal lobe of the mandible is diagnostic.

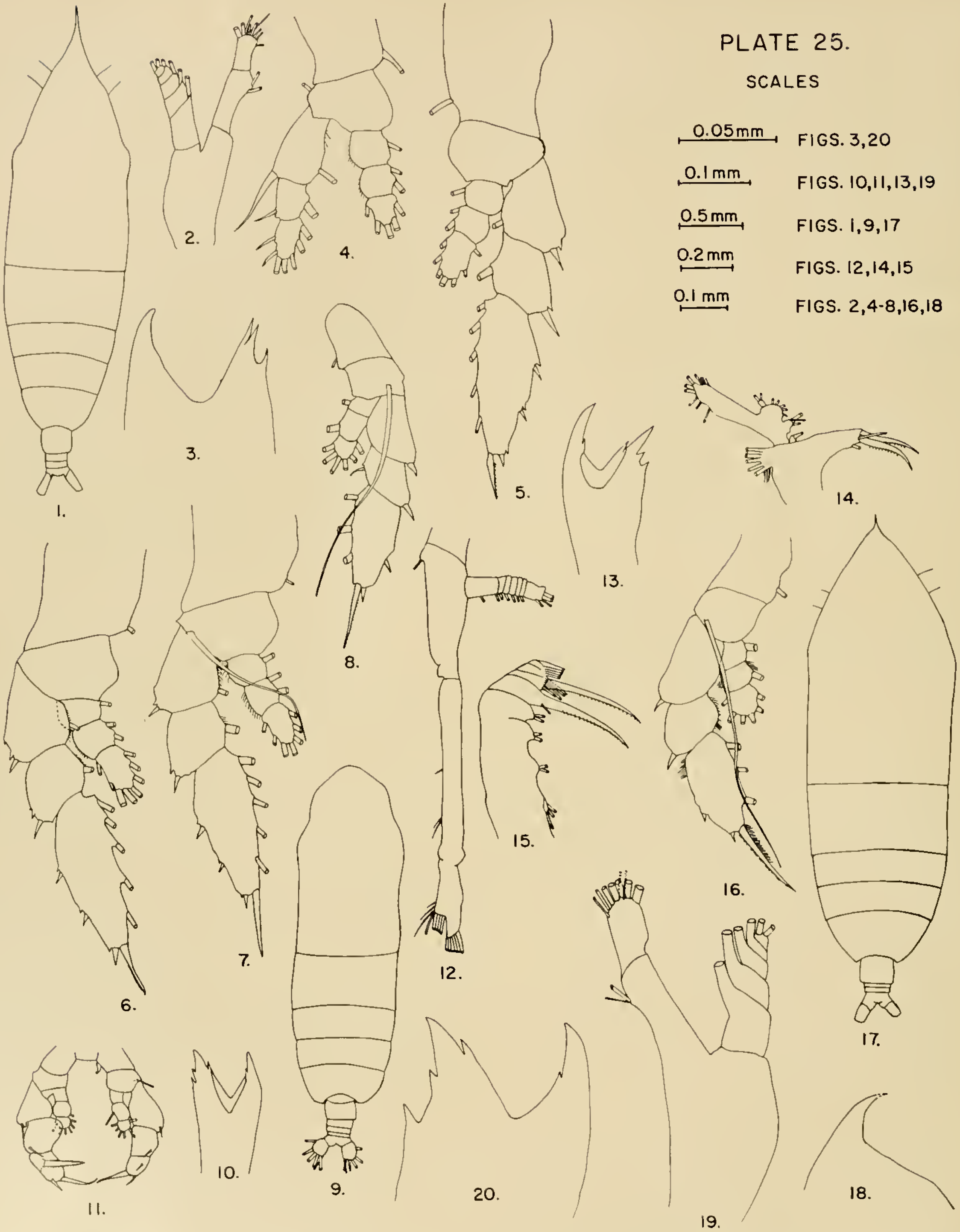

Plate 25.—(1) *Haloptilus acutifrons*, female, dorsal view; (2) mandible palpus; (3) gnathal lobe of mandible; (4) first foot; (5) second foot; (6) third foot; (7) fourth foot; (8) fifth foot; (9) *H. fertilis*, male, dorsal view; (10) gnathal lobe of mandible; (11) fifth pair of feet; (12) *H. ornatus*, female, second antenna; (13) gnathal lobe of mandible; (14) first maxilla; (15) second maxilla; (16) fifth foot; (17) *H. spiniceps*, female, dorsal view; (18) forehead, lateral view; (19) mandible palpus; (20) gnathal lobe of mandible.

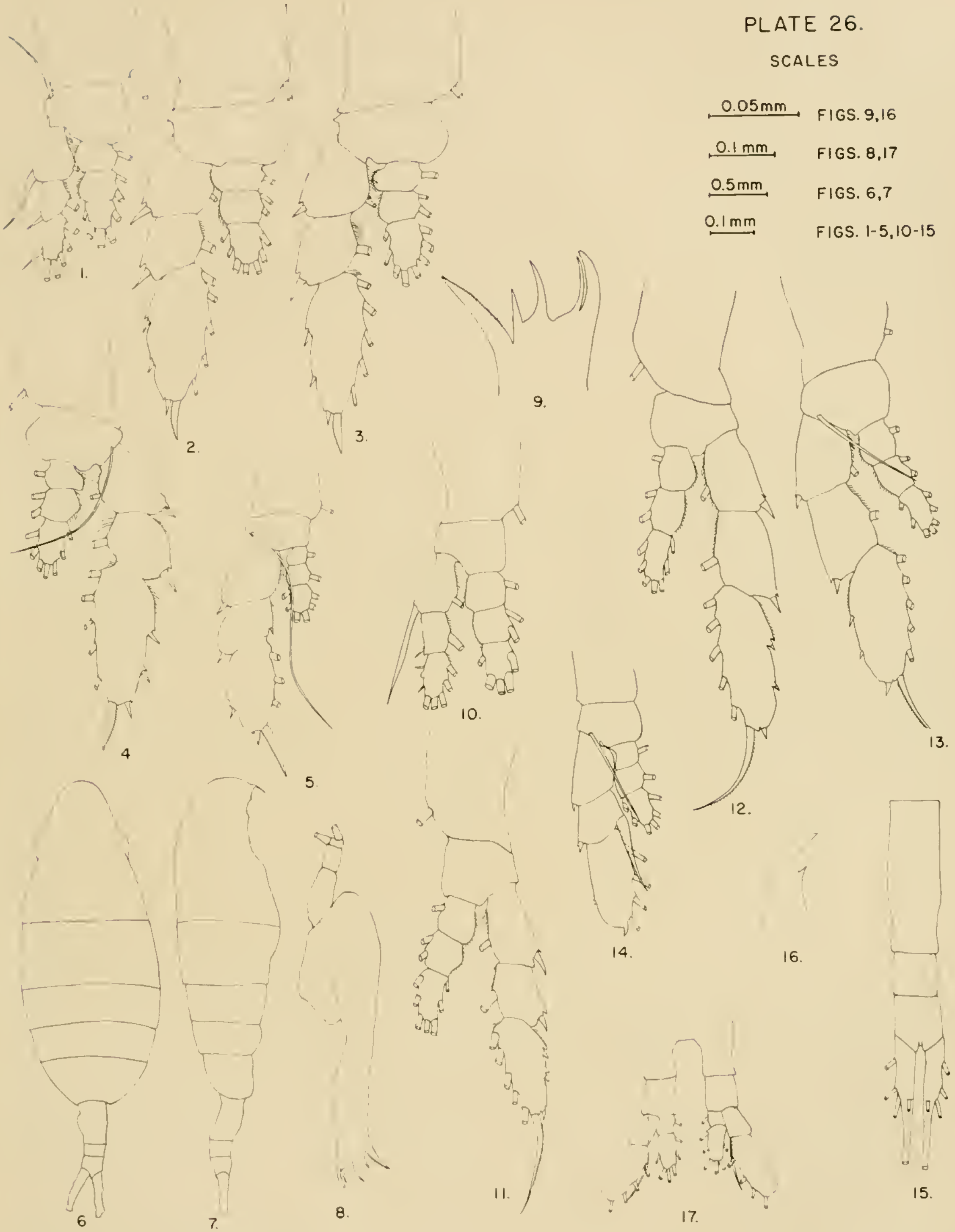

PLATE 26.—(1) *Haloptilus spiniceps*, female, first foot; (2) second foot; (3) third foot; (4) fourth foot; (5) fifth foot; (6) *Augaptilus longicaudatus*, female, dorsal view; (7) lateral view; (8) mandible; (9) gnathal lobe of mandible; (10) first foot; (11) second foot; (12) third foot; (13) fourth foot; (14) fifth foot; (15) *Euaugaptilus hecticus*, female, abdomen; (16) gnathal lobe of mandible; (17) fifth pair of feet.

Augaptilus longicaudatus (Claus, 1863)

(Plate 26, figs. 6–14)

Pacific records: Esterly, 1905; Scott, 1909; Farran, 1929; 1936; Wilson, 1942; Brodsky, 1950; Wilson, 1950; Tanaka, 1953.

Vessel:	*Station*	*Occurrence*
Hugh M. Smith	94	1 female, 3.60 mm.

Remarks: The asymmetrical genital segment (fig. 6), mandibular dentition (fig. 8), and structure of the fifth feet (fig. 14) will identify the female. No males were observed in the present collections.

Euaugaptilus hecticus (Giesbrecht, 1889)

(Plate 26, figs. 15–17)

Pacific records: Farran, 1929; Wilson, 1950; Tanaka, 1953. As *Augaptilus hecticus;* Scott, 1909.

Vessel:	*Station*	*Occurrence*
Hugh M. Smith	31	2 females, 2.70 mm.
Stranger	34	1 female, 2.28 mm.
Satsuma	32	1 female, 2.38 mm.

Remarks: The very long genital segment (fig. 15), claw-like mandibular blade (fig. 16) and the 2-segmented exopods of the fifth feet (fig. 17) serve to identify this species.

Family ARIETELLIDAE

Arietellus setosus Giesbrecht, 1892

(Plate 27, figs. 1–4)

Pacific records: Esterly, 1905; Scott, 1909; Esterly, 1911; Farran, 1929; Johnson, 1942; Wilson, 1942; Brodsky, 1950; Wilson, 1950.

Vessel:	*Station*	*Occurrence*
Hugh M. Smith	63	1 male, 3.99 mm.

Remarks: The posterior thoracic margins are widely divergent (figs. 1, 3) and the forehead terminates in an acute point (fig. 2). Only the male has been found in the present samples.

Arietellus giesbrechti Sars, 1905

(Plate 27, fig. 5)

Pacific records: Wilson, 1950; Tanaka, 1953.

Vessel:	*Station*	*Occurrence*
Hugh M. Smith	29	1 male, 4.75 mm.

Remarks: In the male the left posterior thoracic margin is slightly longer than the right. The fifth feet, shown here (fig. 5), are also diagnostic. No females were observed.

Arietellus plumifer Sars, 1905

(Plate 27, figs. 6–10)

Pacific records: Wilson, 1950.

Vessel:	*Station*	*Occurrence*
Hugh M. Smith	94	1 juvenile female.
Do	63	1 female, 5.51 mm.

Remarks: The posterior margins of the thorax are symmetrical and turned upward (figs. 6, 7, 9), and the head has a small point (figs. 7, 8). No males were found.

Arietellus aculeatus (T. Scott, 1894)

(Plate 27, figs. 11–14)

Pacific records: Scott, 1909; Farran, 1929; Wilson, 1950.

Vessel:	*Station*	*Occurrence*
Hugh M. Smith	63	1 juvenile female, 4.08 mm.

Remarks: The forehead is produced into a long point (fig. 11). The posterior thoracic margins are asymmetrical and the spinous protrusion of the right side is more divergent and longer than the one on the left (figs. 11, 13).

Farran (1929) has suggested that *A. armatus* Wolfenden, 1911 is probably a synonym of *A. aculeatus.* Wilson (1950), however, recognized *armatus* as a valid species and redescribed both sexes.

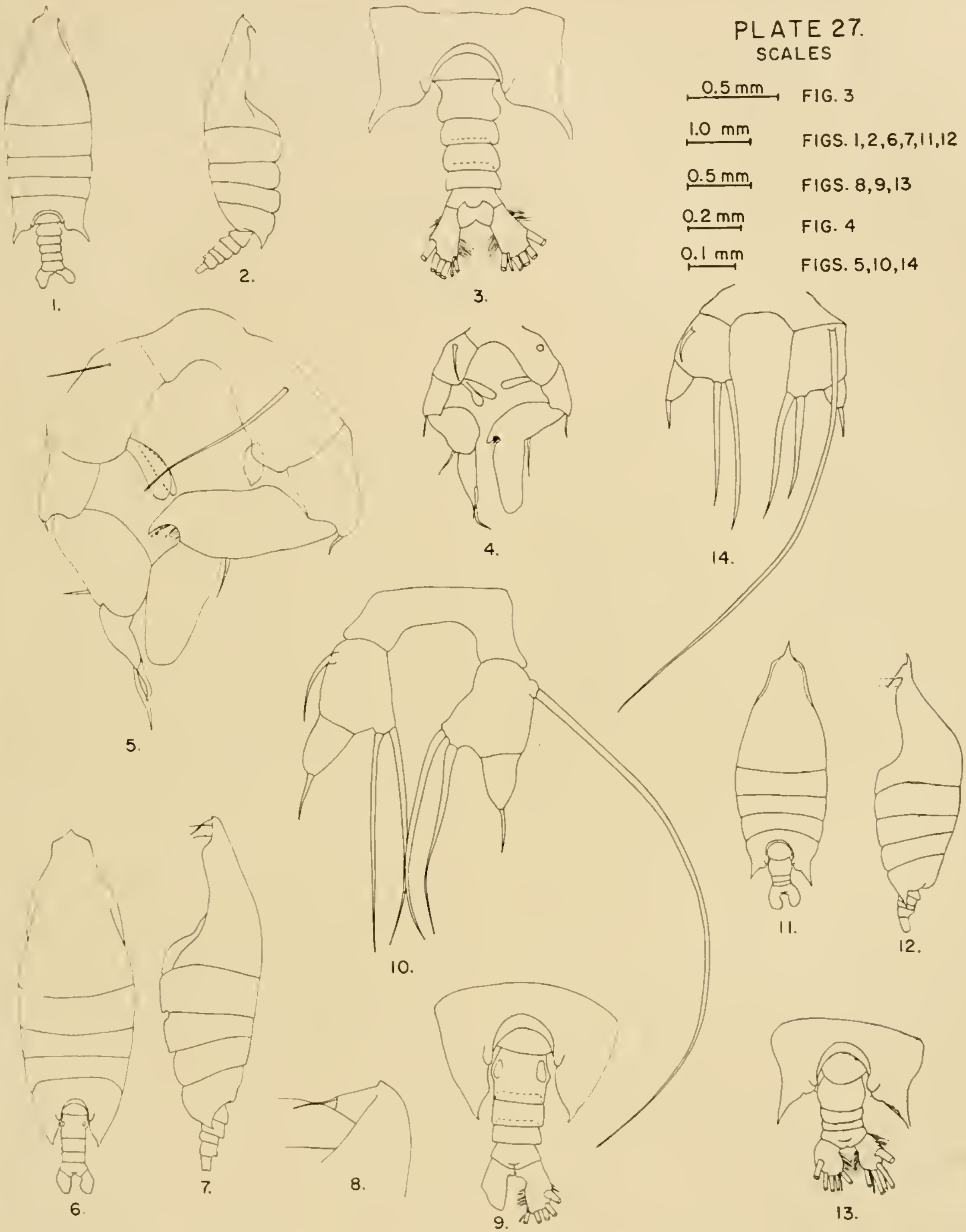

Plate 27.—(1) *Arietellus setosus*, male, dorsal view; (2) lateral view; (3) posterior part of thorax and abdomen, dorsal view; (4) fifth pair of feet; (5) *A. giesbrechti*, male, fifth pair of feet; (6) *A. plumifer*, female, dorsal view; (7) lateral view; (8) forehead, lateral view; (9) posterior part of thorax and abdomen, dorsal view; (10) fifth pair of feet; (11) *A. aculeatus*, juvenile female, dorsal view; (12) lateral view; (13) posterior part of thorax and abdomen, dorsal view; (14) fifth pair of feet.

Family CANDACIIDAE

Candacia longimana (Claus, 1863)

(PLATE 28, FIGS. 1–12)

Pacific records: Scott, 1909; Farran, 1929; 1936; Mori, 1937; 1942; Wilson, 1942; 1950; Honjo, 1952; Tanaka, 1953; Anraku, 1954b; Tsuruta and Chiba, 1954b; Chiba, Tsuruta, and Maéda, 1955; Nagaya et al., 1955; Chiba, 1956; Heinrich, 1957b; Honjo et al., 1957; Yamazi, 1958a.

Vessel:	*Station*	*Occurrence*
Horizon	32	2 females, 2.82, 2.92 mm.; 1 male, 2.69 mm.
Satsuma	32	1 female, 2.89 mm.

Remarks: Twelve species of *Candacia* were found in the collections. For each species, excepting *C. guggenheimi* which has recently been described (Grice and Jones, 1960), I have usually included figures of the dorsal and lateral views of both sexes. Figures are also given of the fifth feet of each species and, for most species, figures of certain of the cephalic appendages (gnathal lobe of the mandible, second maxilla and maxilliped) are given. The females of the species herein described are easily recognized by the forms of the genital segment and fifth feet. The males are recognized by the character of the spine-like protrusion of the right posterior thoracic margin, the structure of the abdomen and the form of the fifth feet.

The female of *C. longimana* has a symmetrical genital segment (fig. 1), the basal tooth of the mandible is tricuspate (fig. 3), and the fifth foot terminates in 3 sub-equal points (figs. 4, 5). The right posterior thoracic margin of the male ends in an irregular protrusion (figs. 6, 7) which in lateral view is seen to turn upward (fig. 9). The right side of the genital segment has a large finger-like protrusion. The right fifth foot is chelate (fig. 11) and the distal margin of the last segment of the left foot ends in 3 small points (fig. 12).

Candacia guggenheimi Grice and Jones, 1960

Pacific records: Grice and Jones, 1960.

Vessel:	*Station*	*Occurrence*
Hugh M. Smith	29	present.

Remarks: This species has recently been described elsewhere (Grice and Jones, 1960). The genital segment of the female has two small spines on the dorsal surface and the genital segment of the male has a bilobed protrusion extending from the right side.

Candacia tenuimana (Giesbrecht, 1889)

(PLATE 28, FIGS. 13–18; PLATE 29, FIGS. 1–4)

Pacific records: Scott, 1909; Johnson, 1942; Wilson, 1942; 1950.

Vessel:	*Station*	*Occurrence*
Hugh M. Smith	29	1 female, 2.07 mm.; 1 male, 2.20 mm.

Remarks: The female genital segment is slightly asymmetrical, the right side being more produced than the left (fig. 13, 15). The basal tooth of the mandible has 2 unequal cusps (fig. 17). The innermost spine-like protrusion of the distal segment of the fifth foot (fig. 18) is considerably longer than the other two. The spine-like protrusion on the right posterior thoracic margin of the male has a bifid tip (fig. 1, 2) and the genital segment is produced to the right in the form of a narrow, curved, spine-like process (fig. 2). As in the preceding species, the right fifth foot is chelate (fig. 4).

Candacia aethiopica (Dana, 1849)

(PLATE 29, FIGS. 5–16)

Pacific records: Streets, 1877; Esterly, 1905; Scott, 1909; Farran, 1929; Yamada, 1933a; Tanaka, 1935b; Farran, 1936; Mori, 1937; Dakin and Colefax, 1940; Johnson, 1942; Mori, 1942; Wilson, 1942; 1950; Tanaka, 1953; Anraku, 1954b; Tsuruta and Chiba, 1954b; Chiba, Tsuruta, and Maéda, 1955; Nagaya et al., 1955; Chiba, 1956; Honjo et al., 1957; Gilmartin, 1958.

Vessel:	*Station*	*Occurrence*
Hugh M. Smith	30	1 male, 2.24 mm.
Horizon	32	1 female, 2.21 mm.; 3 males 2.18–2.24 mm.
Satsuma	32	1 female, 1.97 mm.

Remarks: Of the two spine-like protrusions on the female genital segment, the one on the left is the larger (figs. 5, 7). The basal tooth of the mandible has 3 cusps, the middle one of which is the larger (fig. 9). The distal segment of the fifth foot has 1 external spine, 3

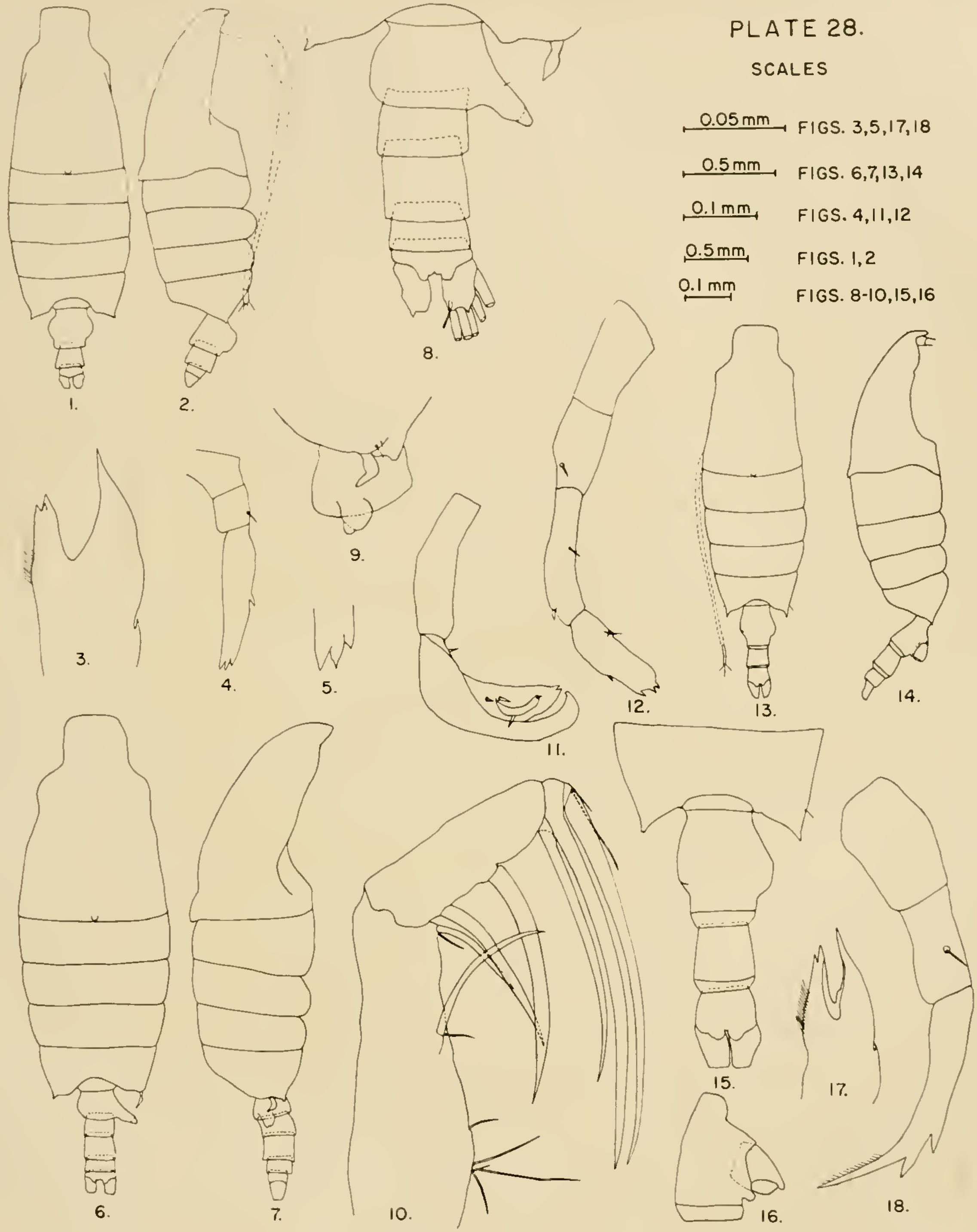

PLATE 28.—(1) *Candacia longimana*, female, dorsal view; (2) lateral view; (3) gnathal lobe of mandible; (4) fifth foot; (5) tip of fifth foot; (6) male, dorsal view; (7) lateral view; (8) abdomen, dorsal view; (9) posterior lateral corner of thorax and genital segment, right side; (10) second maxilla; (11) right fifth foot; (12) left fifth foot; (13) *C. tenuimana*, female, dorsal view; (14) lateral view; (15) posterior part of thorax and abdomen, dorsal view; (16) genital segment, lateral view; (17) gnathal lobe of mandible; (18) fifth foot.

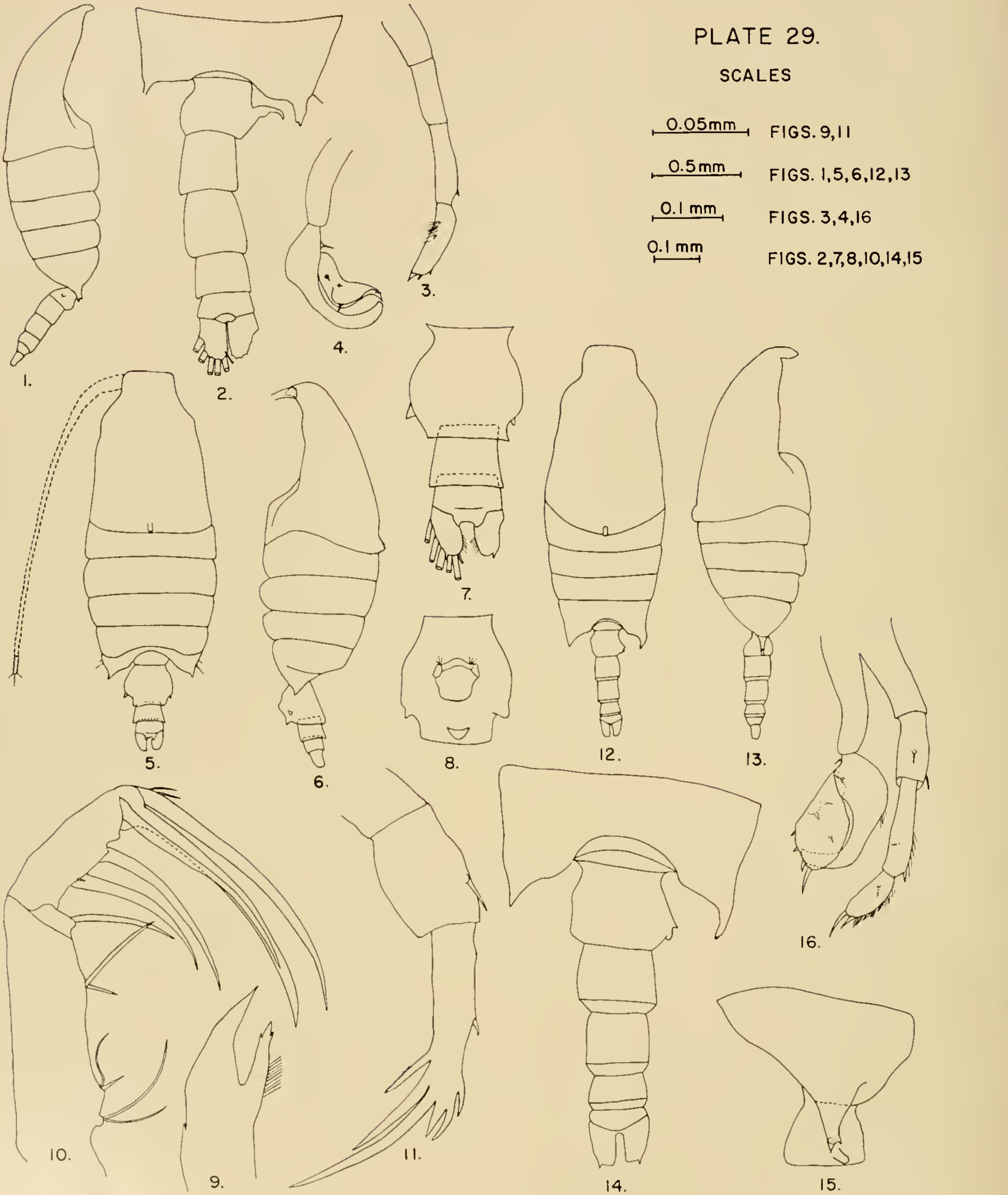

PLATE 29.—(1) *Candacia tenuimana*, male, lateral view; (2) posterior part of thorax and abdomen, dorsal view; (3) left fifth foot; (4) right fifth foot; (5) *C. aethiopica*, female, dorsal view; (6) lateral view; (7) abdomen, dorsal view; (8) genital segment, ventral view; (9) gnathal lobe of mandible; (10) second maxilla; (11) fifth foot; (12) male, dorsal view; (13) lateral view; (14) posterior part of thorax and abdomen, dorsal view; (15) posterior lateral corner of thorax and genital segment, right side; (16) fifth pair of feet.

terminal points and 3 internal, apparently unarticulated, setae (fig. 11). The male has a bifid spine-like protrusion (lateral view) extending from the right posterior margin of the thorax (figs. 13, 15). There is a rounded tubercle and a spine-like point arising from the right side of the genital segment (fig. 14). The chela of the right fifth foot is broad and spinous (fig. 16).

Candacia pachydactyla (Dana, 1849)

(Plate 30, figs. 1–9)

Pacific records: Scott, 1909; Tanaka, 1935; Mori, 1937; Dakin and Colefax, 1940; Wilson, 1942; 1950; Chiba, 1952c; Tanaka, 1953; Tsuruta and Chiba, 1954b; Chiba, Tsuruta, and Maéda, 1955; Hida and King, 1955; Nagaya et al., 1955; Chiba, 1956; Honjo et al., 1957; Yamazi, 1958a.

Vessel:	*Station*	*Occurrence*
Hugh M. Smith	132	2 males, 2.52 mm.
Do	153	1 female, 2.82 mm.; 1 male, 2.07 mm.
Do	178	2 males, 2.52 mm.
Do	30	4 females, 2.48–2.55 mm.; 1 male, 2.48 mm.
Do	63	1 female, 2.88 mm.; 4 males, 2.45–2.72 mm.
Stranger	34	3 females, 2.62–2.65 mm.; 2 males, 2.38, 2.52 mm.
Orsom	10	1 male, 2.48 mm.
Horizon	32	6 females, 2.55–2.62 mm.; 6 males, 2.31–2.55 mm.

Remarks: This is a robust species and is easily distinguished by the coarse spine-like protrusions of the genital segment of the female (figs. 1, 2). The basal tooth of the mandible ends in 3 very unequal cusps (fig. 3). The distal segment of the fifth feet ends in 3 points, the innermost one of which is curved (fig. 4). The right posterior margin of the thorax of the male (figs. 5, 6) is similar to that of *C. aethiopica* but the protrusion of the genital segment is quite large (fig. 7). The thumb of the chela on the right fifth foot ends in a long spine as does the distal segment of the left foot (figs. 8, 9).

Candacia curta (Dana, 1849)

(Plate 30, figs. 10–14; plate 31, figs. 1–3)

Pacific records: Esterly, 1905; Scott, 1909; Farran, 1935b; Farran, 1936; Mori, 1937; Johnson, 1942; Wilson, 1942; 1950; Tanaka, 1953; Tsuruta and Chiba, 1954b; Chiba, Tsuruta, and Maéda, 1955; Nagaya et al., 1955; Chiba, 1956; Honjo et al. 1957; Yamazi, 1958a. As *C. bicornuta;* Mori, 1932.

Vessel:	*Station*	*Occurrence*
Hugh M. Smith	29	2 females, 2.48. 2.62 mm.; 2 males, 2.28, 2.34 mm.
Orsom	10	1 female, 2.44 mm.; 1 male, 2.20 mm.
Horizon	32	1 female, 2.58 mm.

Remarks: The female genital segment is slightly asymmetrical in dorsal view (fig. 10) and has a spine-like protrusion on the ventral side (fig. 11). This spine-like protrusion originates from the right side of the segment (fig. 12). The basal tooth of the mandible has 3 cusps, the lowermost one of which arises from behind the other two (fig. 13). There are 2 points on the distal end of the fifth foot and another point a short distance back of the distal end (fig. 14). The right posterior thoracic margin of the male ends in a hooked spine-like point (fig. 1) and there is a curved, pointed protrusion from the right side of the genital segment (fig. 2). The chela of the fifth foot is also diagnostic (fig. 3).

Candacia bipinnata (Giesbrecht, 1889)

(Plate 31, figs. 4–7)

Synonymy:

Candacia bipinnata (Giesbrecht, 1889, Atti Acc. Lincei Rend., ser. 4, 5 sem. 1: 815).

Candacia pectinata (not of Brady, 1878) Esterly (1905, Univ. Calif. Publ. Zool., 2(4): 193); Mori (1937, The pelagic Copepoda from the neighboring waters of Japan, p. 83); Dakin and Colefax (1940, Publ. Univ. Sydney Dept. Zool. Monogr. 1, p. 105). (*C. pectinata* Brady, 1878=*C. armata* Boeck, 1873.)

Pacific records: Esterly, 1905; Scott, 1909; Tanaka, 1929; Yamada, 1933; Tanaka, 1935b; Mori, 1937; Dakin and Colefax, 1940; Johnson, 1942; Wilson, 1942; Davis, 1949; Motoda, Iizuka, and Anraku, 1950; Brodsky, 1950; Wilson, 1950; Anraku, 1952; Honjo, 1952; Anraku, 1953; Tanaka, 1953; Anraku, 1954b; Chiba, Tsuruta, and Maéda, 1955; Motoda and Anraku, 1955; Nagaya et al., 1955; Chiba, 1956; Honjo et al., 1957;

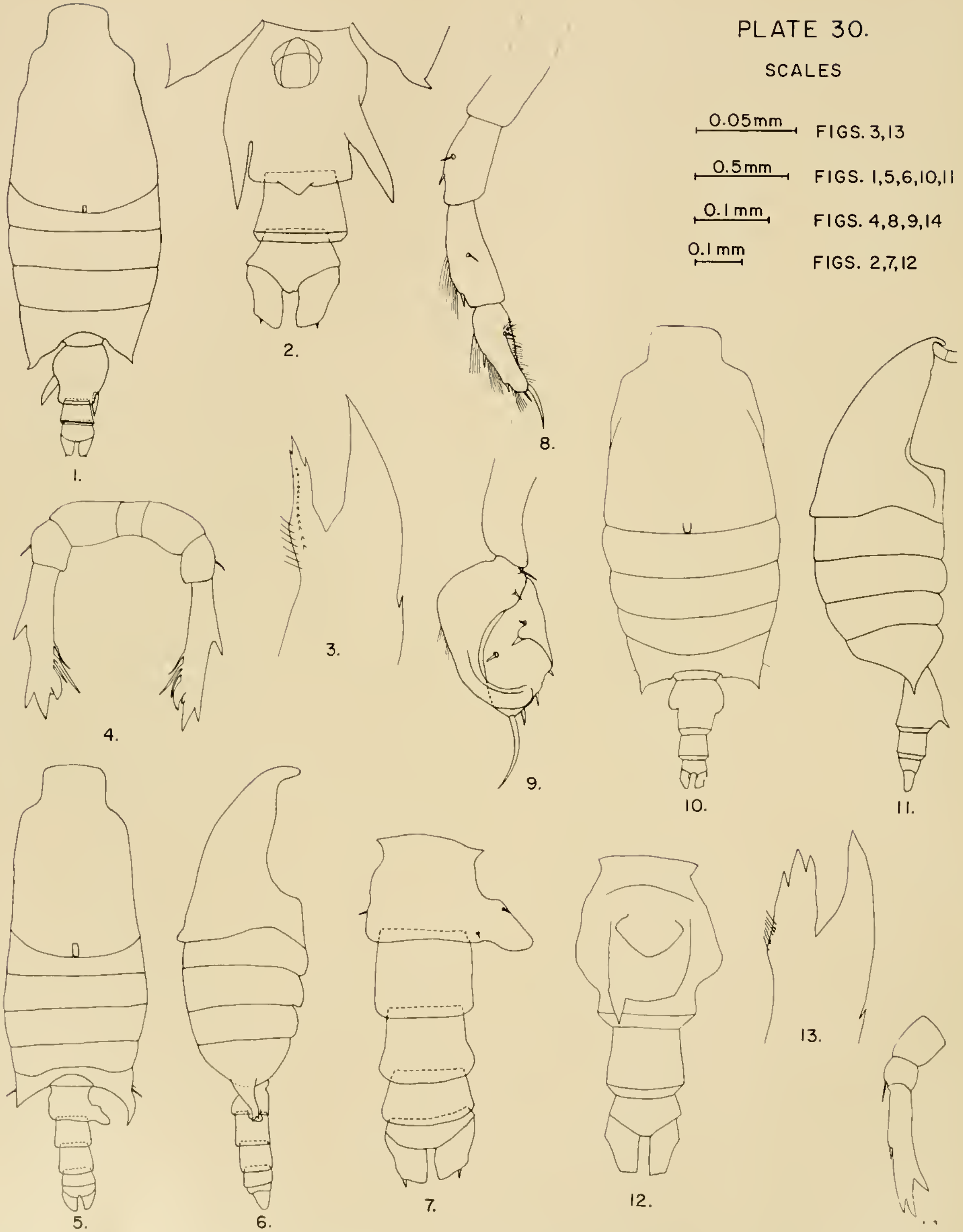

Plate 30.—(1) *Candacia pachydactyla*, female, dorsal view; (2) abdomen, ventral view; (3) gnathal lobe of mandible; (4) fifth pair of feet; (5) male, dorsal view; (6) lateral view; (7) abdomen, dorsal view; (8) left fifth foot; (9) right fifth foot; (10) *C. curta*, female, dorsal view; (11) lateral view; (12) abdomen, ventral view; (13) gnathal lobe of mandible; (14) fifth foot.

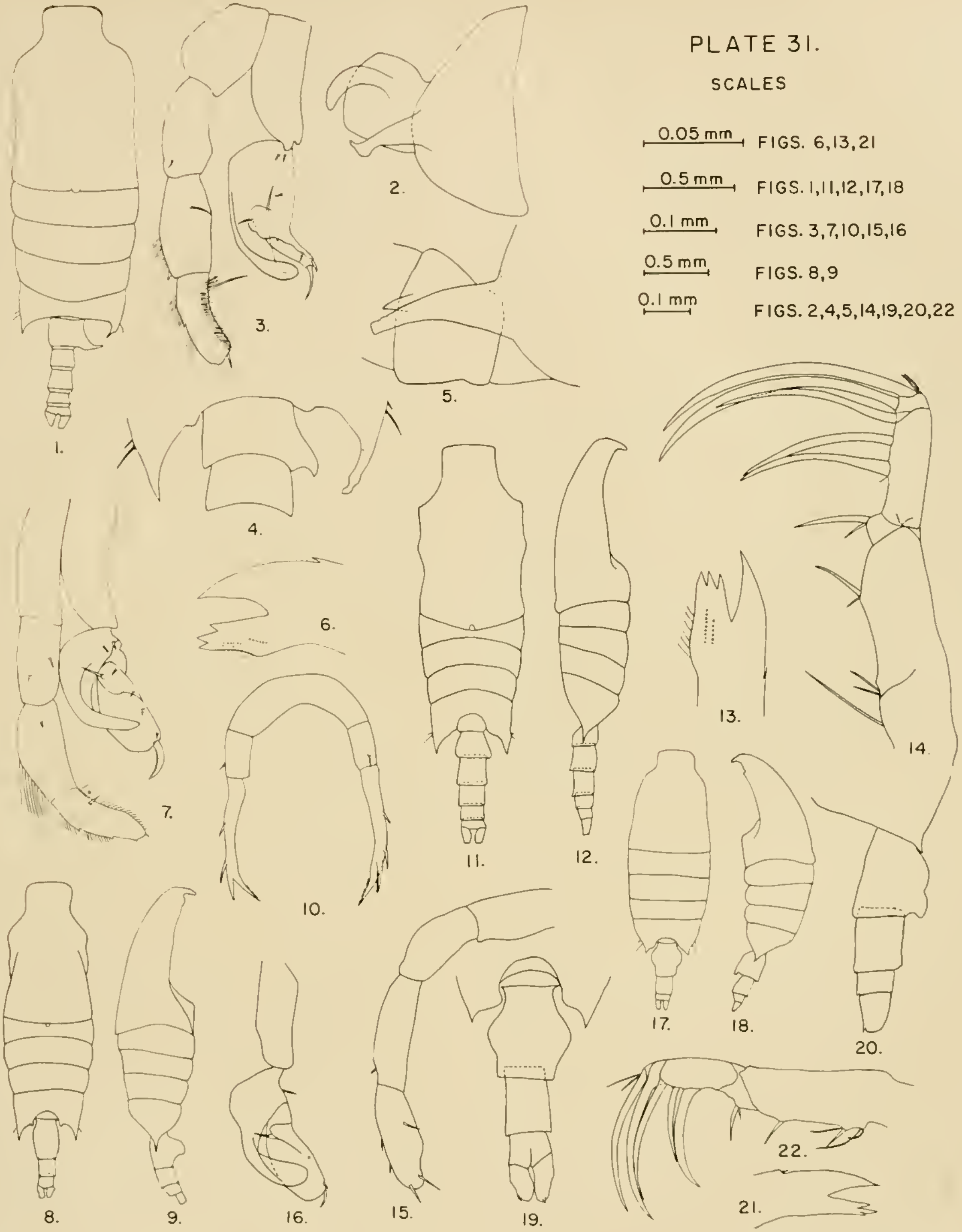

PLATE 31.—(1) *Candacia curta*, male, dorsal view; (2) posterior part of thorax and genital segment, right side; (3) fifth pair of feet; (4) *C. bipinnata*, male, posterior part of thorax and abdomen, dorsal view; (5) posterior part of thorax and abdomen, right side; (6) gnathal lobe of mandible; (7) fifth pair of feet; (8) *C. varicans*, female, dorsal view; (9) lateral view; (10) fifth pair of feet; (11) male, dorsal view; (12) lateral view; (13) gnathal lobe of mandible; (14) second maxilla; (15) left foot; (16) right foot; (17) *C. catula*, female, dorsal view; (18) lateral view; (19) abdomen, dorsal view; (20) abdomen, lateral view; (21) gnathal lobe of mandible; (22) second maxilla.

Yamazi, 1958a; Brodsky, 1959; Lindberg, 1959. As *C. bipunctata* [=*C. bipinnata*?]; Yamazi, 1953a.

Vessel:	*Station*	*Occurrence*
Hugh M. Smith	178	1 male, 1.90 mm.
Do	144	1 male, 2.28 mm.

Remarks: Only two males of this species were found. The right posterior lateral protrusion of the thorax is characteristic. This protrusion exceeds the end of the genital segment and its tip, as seen in dorsal view, is irregular (fig. 4). In lateral view the distal end appears to be somewhat truncate (fig. 5). A small, posteriorly directed hook arises from the right side of the genital segment (fig. 4). The basal tooth of the gnathal lobe of the mandible is tricuspate (fig. 6). The thumb of the chela of the right fifth foot has a stout spine at its tip.

In regard to the above indicated synonymy, Sars (1903) redescribed *C. armata* (Boeck, 1873) and pointed out that *C. pectinata* (Brady, 1878) is a synonym of the former species. *C. armata* is a north Atlantic species which occurs along the east coast of the United States as far south as off Beaufort, North Carolina (Fleminger and Bowman, 1956), and along the coast of Europe probably as far south as off Spain. It has also been reported from the Mediterranean Sea (Rose, 1934) and from the Adriatic Sea (Hure, 1955).

I have examined specimens identified by Esterly (1905) and labeled *C. bipinnata* ♀, *C. pectinata* ♂, which were loaned to me by Dr. Abraham Fleminger of the Scripps Institution of Oceanography. Included in the vial were two females, *C. bipinnata*. Esterly's figure of the fifth foot of his female *C. pectinata* is probably that of a stage V female *C. bipinnata*, a species which also occurred in his collections. The figure of the genital segment of his male *C. pectinata* is clearly referable to *C. bipinnata*. Esterly stated in regard to *C. bipinnata* that he did not find the male of this species.

Mori (1937) reported only the male of *C. pectinata* from Japanese waters. His figures and description of this species indicate that it is actually *C. bipinnata*. The protrusion of the right posterior lateral margin of the thorax, the form of the hook on the right side of the genital segment, and the structure of the fifth pair of feet all agree with those of *C. bipinnata*. Mori also presented figures of male *C. bipinnata* which are not unlike those of his *C. pectinata*.

Dakin and Colefax's (1940) *C. pectinata* (both sexes) which were questionably referred to this species are also *C. bipinnata*. I have examined specimens which were obtained from the east coast of Australia and which are similar to the figures presented by these authors for *C. pectinata*. These copepods are stage V female and adult male *C. bipinnata*.

As to other reports of *C. pectinata* from the Pacific Ocean, Scott (1909) has previously stated that Brady's (1883) figures of this species "represents at least four distinct species, none of which are identical with it" (*C. pectinata*=*C. armata*). *C. pectinata* has also been reported by Honjo (1952) and Honjo et al. (1957). As the species is included in lists, without descriptions or figures, these records too are questionable and in need of confirmation.

Candacia varicans (Giesbrecht, 1892)

(PLATE 31, FIGS. 8–16)

Pacific records: Farran, 1929; Johnson, 1942; Wilson, 1942; 1950.

Vessel:	*Station*	*Occurrence*
Hugh M. Smith	31	2 males, 2.14, 2.18 mm.
Do	63	1 female, 2.55 mm.; 2 males, 2.26, 2.28 mm.

Remarks: The female has a long and symmetrical genital segment (fig. 8) which is produced on the ventral side (fig. 9). The fifth feet are slightly asymmetrical and terminate in two rather long, but unequal, points (fig. 10). The thorax and genital segment of the male are symmetrical (figs. 11, 12). The basal tooth of the mandible ends in three approximately equal cusps. The right fifth foot is chelate (fig. 16).

Candacia catula (Giesbrecht, 1889)

(PLATE 31, FIGS. 17–22; PLATE 32, FIGS. 1–6)

Pacific records: Scott, 1909; Tanaka, 1935b; Farran, 1936; Mori, 1937; Dakin and Colefax, 1940; Mori, 1942; Wilson, 1942; Anraku, 1952; Tanaka, 1953;

Tsuruta and Chiba, 1954b; Chiba, Tsuruta, and Maéda, 1955; Nagaya et al., 1955; Yamazi, 1958a.

Vessel:	*Station*	*Occurrence*
Hugh M. Smith	178	present.
Do	63	2 females, 1.56, 1.63 mm.; 2 males, 1.46, 1.53 mm.
Stranger	34	7 females, 1.60–1.67 mm.; 2 males, 1.53, 1.62 mm.
Orsom	10	1 female, 1.53 mm.; 1 male, 1.43 mm.
Horizon	32	1 female, 1.59 mm.

Remarks: This is a small species, the females of which have a symmetrical genital segment (figs. 17, 19). The ventral surface is produced into a lobe (figs. 18, 20). The basal tooth of the mandible ends in 3 cusps, the lowermost one of which is quite small (fig. 21). The fifth foot terminates in 3 unequal points (fig. 1). The male posterior thoracic margins are symmetrical (figs. 2, 4) and the chela of the right fifth foot is small. The thumb of the chela has a long spine protruding from its tip (fig. 6).

Candacia bispinosa (Claus, 1863)

(Plate 32, figs. 7–14)

Pacific records: Scott, 1909; Farran, 1929; Tanaka, 1935b; Farran, 1936; Mori, 1937; Johnson, 1942; Wilson, 1942; 1950; Honjo, 1952; Tanaka, 1953; Anraku, 1954b; Tsuruta and Chiba, 1954b; Chiba, Tsuruta, and Maéda, 1955; Motoda and Anraku, 1955; Nagaya et al., 1955; Chiba, 1956; Heinrich, 1957b; Honjo et al., 1957; Heinrich, 1958a; Yamazi, 1958a.

Vessel:	*Station*	*Occurrence*
Hugh M. Smith	153	3 females, 1.66–1.80 mm.
Do	178	1 female, 1.60 mm.
Stranger	34	1 female, 1.67 mm.; 1 male, 1.73 mm.
Orsom	10	1 female, 1.56 mm.; 1 male, 1.56 mm.
Satsuma	32	1 male, 1.70 mm.

Remarks: This species and the following two species, *C. simplex* (Giesbrecht) and *C. truncata* (Dana), differ in a few details (e.g., structure of right, first antenna in male and fifth feet in both sexes) from the preceding nine species. It has been suggested by Sars (1903) that these three may have to be removed from the genus *Candacia*.

The female of *C. bispinosa* has two spine-like protrusions arising from the genital segment (fig. 7). These protrusions, particularly the one on the left side, are quite variable in shape and in size. In one specimen (*Smith* 178) the left protrusion reaches nearly to the anal segment. There is a small rounded knob arising from the ventral side of the genital segment near the posterior end (fig. 8). The pre-anal segment is asymmetrical. The left side is dilated near the anterior end, but there is some variation in the size of the protrusion. The ventral surface of this segment may or may not have a row of hairs arising from near the posterior end. The basal tooth of the mandible is undivided, but one or more spine-like processes are present on this tooth (fig. 9). The large terminal finger-like protrusion of the distal segment of the fifth foot is finely serrate on both sides (fig. 12).

Segment 20 of the right first antenna of the male is swollen distally (fig. 13). There are 3 outer edge spines on the distal segment of the right fifth foot (fig. 14). The proximal spine is shorter than the distal two spines. The penultimate segment of the left fifth foot is enlarged and the outer edge seta of the distal segment is shorter than the terminal ones.

Candacia simplex (Giesbrecht, 1889)

(Plate 32, figs. 15–18; plate 33, figs. 1–5)

Pacific records: Scott, 1909; Farran, 1929; 1936; Mori, 1937; Johnson, 1942; Mori, 1942; Wilson, 1942; 1950; Tanaka, 1953; Tsuruta and Chiba, 1954b; Chiba, Tsuruta, and Maéda, 1955; Nagaya et al., 1955; Rose, 1955; Chiba, 1956.

Vessel:	*Station*	*Occurrence*
Hugh M. Smith	94	1 female, 1.93 mm.
Do	132	8 females, 1.73–1.87 mm.; 3 males 1.73–1.83 mm.
Do	144	present.
Do	153	1 female, 1.67 mm.
Do	178	2 females, 1.90 mm.; 1 male, 1.80 mm.

Remarks: The genital segment of the female is slightly asymmetrical and has a group of small hair-like structures which are visible on the right side (figs. 15, 16). The terminal finger of the distal segment of the fifth foot is

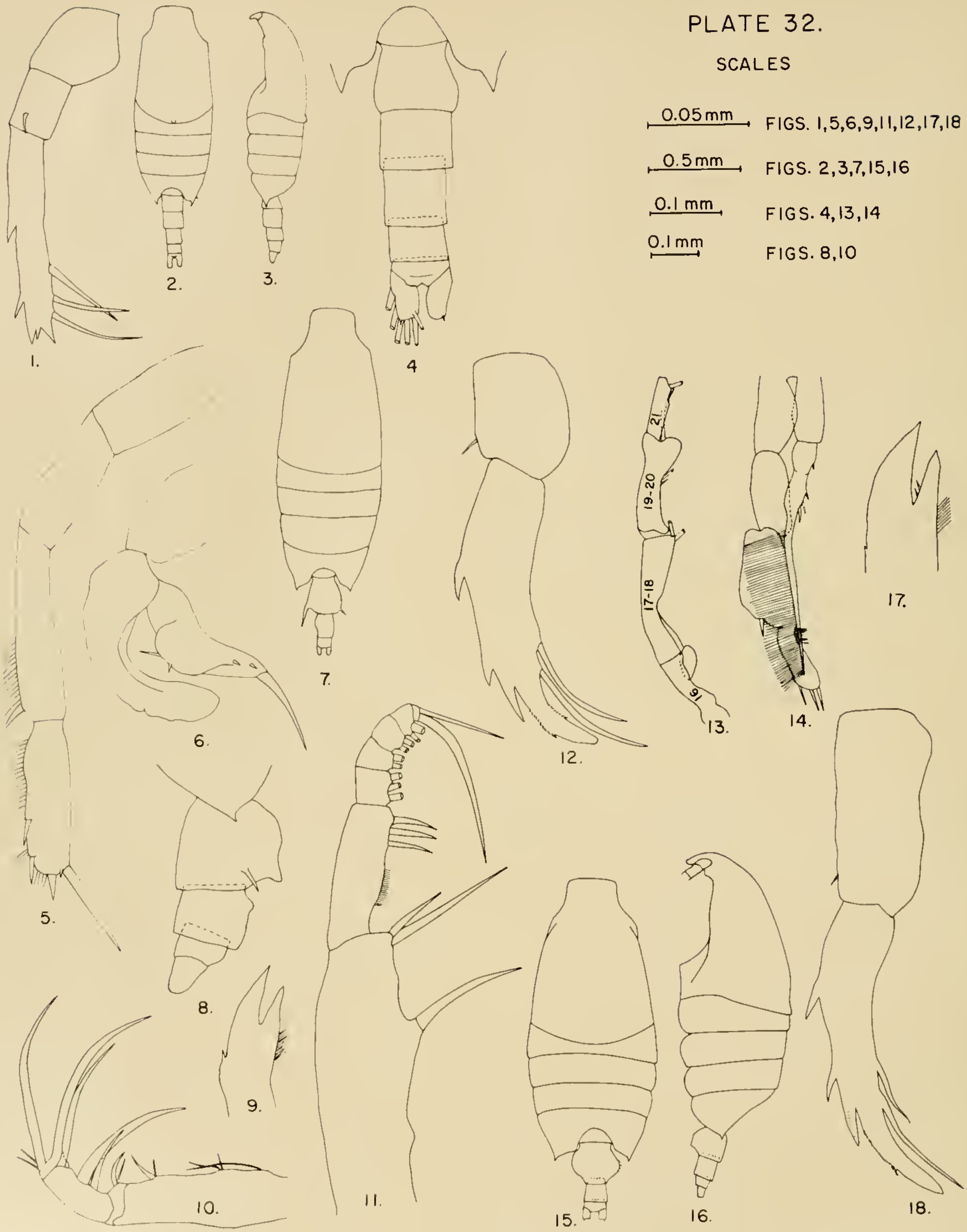

Plate 32.—(1) *Candacia catula*, female, fifth foot; (2) male, dorsal view; (3) lateral view; (4) abdomen, dorsal view; (5) left fifth foot; (6) right fifth foot; (7) *C. bispinosa*, female, dorsal view; (8) abdomen, right side; (9) gnathal lobe of mandible; (10) second maxilla; (11) maxilliped; (12) fifth foot; (13) male, segments 16 to 21 of right first antenna; (14) fifth pair of feet; (15) *C. simplex*, female, dorsal view; (16) lateral view; (17) gnathal lobe of mandible; (18) fifth foot.

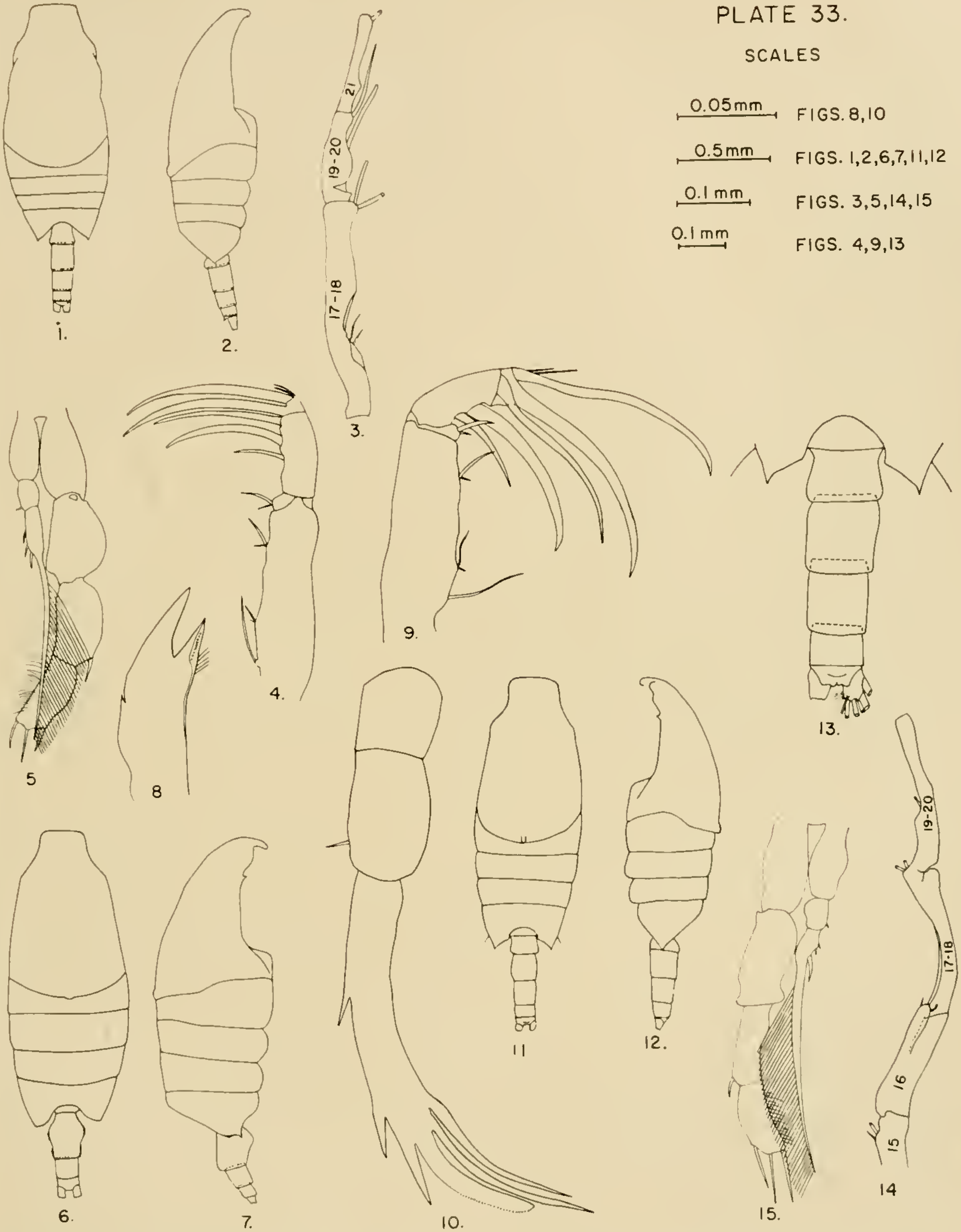

PLATE 33.—(1) *Candacia simplex*, male, dorsal view; (2) lateral view; (3) segments 17 to 21 of right first antenna; (4) second maxilla; (5) fifth pair of feet; (6) *C. truncata*, female, dorsal view; (7) lateral view; (8) gnathal lobe of mandible; (9) second maxilla; (10) fifth foot; (11) male, dorsal view; (12) lateral view; (13) abdomen, dorsal view; (14) segments 15 to 20 of right first antenna; (15) fifth pair of feet.

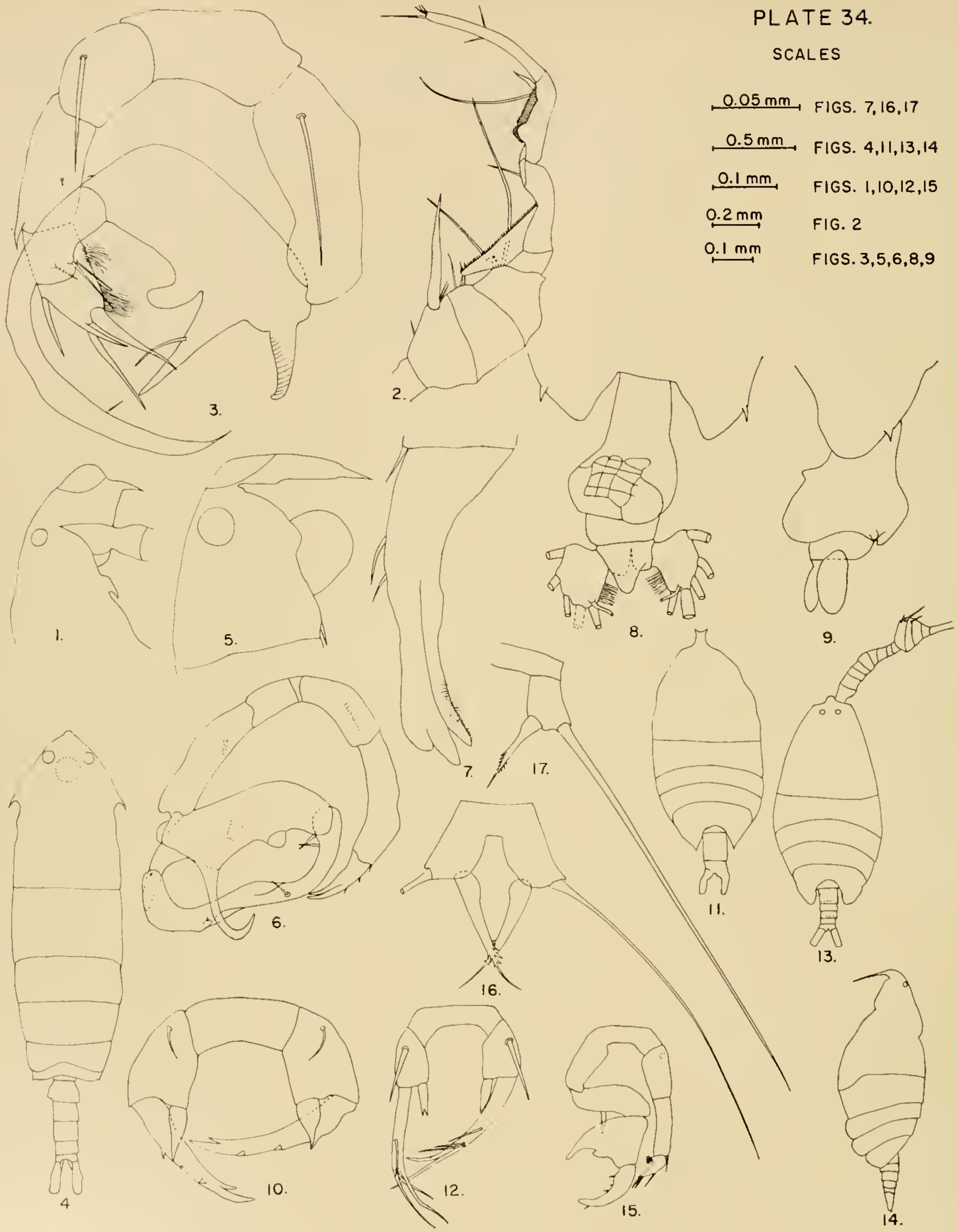

PLATE 34.—(1) *Pontella securifer*, male, forehead, lateral view; (2) distal end of right first antenna; (3) fifth pair of feet; (4) *P. tenuiremis*, male, dorsal view; (5) forehead, lateral view; (6) fifth pair of feet; (7) left fifth foot; (8) *Labidocera detruncata*, female, abdomen, dorsal view; (9) lateral view; (10) fifth pair of feet; (11) *Pontellina plumata*, female, dorsal view; (12) fifth pair of feet; (13) male, dorsal view; (14) lateral view; (15) fifth pair of feet; (16) *Acartia danae*, female, fifth foot; (17) *A. negligens*, female, fifth pair of feet.

finely serrate on the external margin (fig. 18). Of the 2 internal setae on this segment, the distal one is approximately twice the length of the proximal one. The male thorax and abdomen are symmetrical (figs. 1, 2). The right fifth foot is similar to that of *C. bispinosa* (fig. 5). The left fifth foot terminates in 3 setae, the middle one of which is the longer. The penultimate segment is not particularly enlarged.

Candacia truncata (Dana, 1849)

(Plate 33, figs. 6–14)

Pacific records: Scott, 1909; Yamada, 1933a; Tanaka, 1935b; Farran, 1936; Mori, 1937; Dakin and Colefax, 1940; Mori, 1942; Wilson, 1942; Tanaka, 1953; Anraku, 1954b; Tsuruta and Chiba, 1954b; Chiba, Tsuruta, and Maéda, 1955; Motoda and Anraku, 1955; Nagaya et al., 1955; Chiba, 1956; Heinrich, 1957b; Honjo et al., 1957; Yamazi, 1958a; 1958b; Grice and Jones, 1960. As *C. turgida;* Wilson, 1950.

Vessel:	*Station*	*Occurrence*
Hugh M. Smith	132	3 females, 1.90–2.00 mm.; 2 males, 2.11 mm.
Do	153	3 males, 1.97–2.11 mm.
Do	30	present.
Do	63	1 female, 1.87 mm.
Stranger	34	7 females, 1.94–2.04 mm.; 3 males, 1.94–1.97 mm.
Orsom	10	3 females, 1.97–2.04 mm.; 1 male, 2.06 mm.
Horizon	32	11 females, 1.84–2.00 mm.; 5 males, 1.94–2.00 mm.
Satsuma	32	5 females, 1.87–1.90 mm.; 3 males, 1.87–2.00 mm.

Remarks: The female genital segment is symmetrical and finely pubescent on the lateral margins (fig. 16). The terminal finger of the distal segment of the fifth foot is finely serrate along its outer distal margin (fig. 10). The proximal seta on the internal margin is slightly shorter than the distal one. The male thorax and abdomen are symmetrical (figs. 11, 12). Segment 16 of the right first antenna is produced into an elongate process (fig. 14). The distal spine on the terminal segment of the right fifth foot (fig. 15) is considerably larger than the preceding two spines. The terminal seta on some specimens is articulated to this segment while in others it is not.

Family PONTELLIDAE

Pontella securifer Brady, 1883

(Plate 34, figs. 1–3)

Pacific records: Scott, 1909; Farran, 1936; Dakin and Colefax, 1940; Wilson, 1942; 1950; Tanaka, 1953.

Vessel:	*Station*	*Occurrence*
Hugh M. Smith	30	2 females, 4.40, 4.46 mm.
Do	31	1 male, 4.40 mm.

Remarks: Both sexes have a large lens situated at the base of the rostrum. Figures of the male sex are given (figs. 1–3).

Pontella tenuiremis Giesbrecht, 1889

(Plate 34, figs. 4–7)

Pacific records: Wilson, 1942; 1950.

Vessel:	*Station*	*Occurrence*
Horizon	32	1 male, 2.80 mm.

Remarks: The structure of the fifth feet (figs. 6, 7) distinguishes the male of this species from other *Pontella*. No females were found.

Labidocera detruncata (Dana, 1849)

(Plate 34, figs. 8–10)

Pacific records: Scott, 1909; Yamada, 1933; Farran, 1936; Mori, 1937; Dakin and Colefax, 1940; Mori, 1942; 1950; Tanaka, 1953; Anraku, 1954b; Chiba, Tsuruta, and Maéda, 1955; Nagaya et al., 1955; Chiba, 1956; Yamazi, 1958a; 1958b.

Vessel:	*Station*	*Occurrence*
Hugh M. Smith	30	1 female, 2.72 mm.
Do	32	1 female, 2.68 mm.

Remarks: The lateral margins of the last thoracic segment (figs. 8, 9) are pointed and the genital segment is asymmetrical. These two characters plus the structure of the fifth feet (fig. 10) will identify the female. No male was found in the present collections.

Pontellina plumata (Dana, 1849)

(Plate 34, figs. 11–15)

Pacific records: Scott, 1909; Farran, 1929; 1936; Mori, 1937; Dakin and Colefax, 1940; Mori, 1942; Wilson, 1950; Anraku, 1952; Tanaka, 1953; Anraku, 1954b; Tsuruta and Chiba, 1954b; Chiba, Tsuruta, and Maéda, 1955; Motoda and Anraku, 1955; Nagaya et al., 1955; Chiba, 1956; Heinrich, 1958a; Yamazi, 1958a.

Vessel:	*Station*	*Occurrence*
Hugh M. Smith	132	1 female, 1.66 mm.; 2 males, 1.49, 1.59 mm.
Do	178	present.
Do	30	9 females, 1.43–1.84 mm.; 1 male, 1.56 mm.
Do	31	2 females, 1.62, 1.80 mm.
Do	63	present.
Stranger	34	2 females, 1.56, 1.63 mm.
Orsom	10	present.
Horizon	32	present.

Remarks: The female is distinguished by the symmetrically pointed posterior margins of the last thoracic segment (fig. 11) and the right furca. This furca is fused to the anal segment. The posterior lateral margins of the last thoracic segment of the male are rounded (figs. 13, 14) and the right fifth foot is chelate (fig. 15).

Family ACARTIIDAE

Acartia danae Giesbrecht, 1889

(Plate 34, fig. 16)

Pacific records: Scott, 1909; Farran, 1929; 1936; Mori, 1937; Dakin and Colefax, 1940; Johnson, 1942; Mori, 1942; Wilson, 1942; Davis, 1949; Wilson, 1950; Anraku, 1952; Tanaka, 1953; Anraku, 1954b; Motoda and Anraku, 1955; Heinrich, 1957b; Honjo et al., 1957; Heinrich, 1958a; Yamazi, 1958a; 1958b.

Vessel:	*Station*	*Occurrence*
Hugh M. Smith	94	present.
Do	132	1 female, 1.12 mm.
Do	178	present.

Remarks: The female has a large spine on the first segment of the first antennae and the posterior lateral margins of the thorax end in a large point. The external seta on the fifth foot (fig. 16) is slightly more than twice the length of the internal spine.

Acartia negligens Dana, 1849

(Plate 34, fig. 17)

Pacific records: Scott, 1909; Farran, 1929; 1936; Mori, 1937; 1942; Wilson, 1942; 1950; Anraku, 1952; Honjo, 1952; Tanaka, 1953; Anraku, 1954b; Tsuruta and Chiba, 1954b; Chiba, Tsuruta, and Maéda, 1955; Motoda and Anraku, 1955; Nagaya et al., 1955; Chiba, 1956; Heinrich, 1957b; 1958a; Yamazi, 1958a; 1958b.

Vessel:	*Station*	*Occurrence*
Hugh M. Smith	153	2 females, 1.05, 1.10 mm.
Do	178	present.
Do	30	10 females, 1.08–1.21 mm.
Do	31	5 females, 1.10–1.17 mm.
Do	63	present.
Stranger	34	2 females, 1.08, 1.12 mm.
Orsom	10	14 females, 1.10–1.16 mm.
Satsuma	32	present.

Remarks: In contradistinction to *A. danae*, the posterior lateral margins of the last thoracic segment have a series of very small points. The external seta on the fifth foot (fig. 17) is more than four times the length of the internal spine.

LITERATURE CITED

ANRAKU, M.

1952. Plankton copepods collected by R. S. *Yushino-Maru* in Pacific waters to the east of northern Japan during her cruise in November, 1948. Bulletin of the Faculty of Fisheries. Hokkaido University 3(1): 31–39. [In Japanese.]

1953. Seasonal distribution of pelagic copepods at Oshora Bay, west coast of Hokkaido. Bulletin of the Faculty of Fisheries. Hokkaido University 3(3): 187–192.

1954a. Distribution of plankton copepods off Kitami, Hokkaido, in Okhotsk Sea in summer, 1949 and 1950. Bulletin of the Faculty of Fisheries. Hokkaido University 4(4): 249–255.

1954b. Copepods collected on the whaling grounds off northern Japan and Bonin Islands. Bulletin of the Faculty of Fisheries. Hokkaido University 5(1): 1–8.

1954c. Gymnoplea Copepoda collected in Aleutian waters in 1953. Bulletin of the Faculty of Fisheries. Hokkaido University 5(2): 123–136.

AUSTIN, T. S.

1957. Summary, oceanographic and fishery data, Marquesas Islands area, August-September, 1956 (Equapac). U.S. Fish and Wildlife Service, Special Scientific Report—Fisheries No. 217, 186 p.

BARY, B. M.

1959. Species of zooplankton as a means of identifying different surface waters and demonstrating their movements and mixing. Pacific Science 13(1): 14–54.

BERNARD, M.

1958. Révision des *Calocalanus* (Copépodes Calanoida) avec description d'un genre nouveau et deux espèces nouvelles. Bulletin de la Société zoologique de France 83(2–3): 185–199.

BOECK, A.

1873. Nye slaegter og arter af saltvands-copepoder. Christiania Videnskabs-Selskabet Forhanlinger, p. 37–60.

BOWMAN, T. E.

1955. A new copepod of the genus *Calanus* from the northeastern Pacific with notes on *Calanus tenuicornis* Dana. Pacific Science 9(4): 413–422.

1958. A new species of *Acrocalanus* (Copepoda: Calanoida) from off the southeastern coast of the United States. Bulletin of Marine Science of the Gulf and Caribbean 8(2): 118–124.

BRADY, G. S.

1878. A monograph of the free and semi-parasitic Copepoda of the British Islands. Vol. 1. The Ray Society, p. 1–148.

1883. Report on the Copepoda collected by *H.M.S. Challenger* during the years 1873–76. Report on the Scientific Results of *HMS Challenger*, Zoology. Vol. 8, p. 1–142.

1899. On the marine Copepoda of New Zealand. Transactions of the Zoological Society of London 15, pt. 2:31–54.

BRODSKY, K. A.

1950. Calanoida of polar and far eastern seas of the U.S.S.R. Opredeliteli po Fauna S.S.S.R., Izdavaemi, Zoologicheskim Institutom Akademii Nauk SSSR. 35: 1–442. [In Russian.]

1952. On the vertical distribution of copepods in the northwestern Pacific Ocean. Investigations of the far eastern seas of the U.S.S.R. *III*. Deep water fauna of the northwestern Pacific Ocean, p. 88–94. [Translated by W. G. Van Campen, 1956, U.S. Fish and Wildlife Service, Special Scientific Report—Fisheries No. 192, p. 1–6.]

1955. Plankton of the northwestern part of the Kuroshio and waters of the Pacific Ocean adjacent to the Kurile Islands. Transactions of the Institute of Oceanology, Academy of Sciences, U.S.S.R. 18: 124–133. [Translated by W. G. Van Campen, 1956, U.S. Fish and Wildlife Service, Special Scientific Report—Fisheries No. 192, p. 16–24.]

1959. Zooplankton of sea waters of south Sakhalin and south Kurile Islands. Investigations of Far Eastern Seas VI, Academy of Sciences, U.S.S.R., p. 5–46. [In Russian.]

CAMPBELL, M. H.

1929. Some free swimming copepods of the Vancouver Island region. Transactions of the Royal Society of Canada 23, pt. 2, sect. 5: 303–332.

CHIBA, T.

1949. On the distribution of the plankton in the eastern China Sea and Yellow Sea. I. Plankton composition in spring. The Journal of the Shimonoseki College of Fisheries 1(1): 57–63. [In Japanese.]

1952a. On the distribution of the plankton in the eastern China Sea and Yellow Sea. II. Observation on the plankton in spring during the period 1949–50. Bulletin of the Japanese Society of Scientific Fisheries 17(7): 183–186. [In Japanese.]

1952b. On the distribution of the plankton in the eastern China Sea and Yellow Sea. III. Observations on the plankton in autumn during the years 1948–1949. Bulletin of the Japanese Society of Scientific Fisheries 17(7): 187–190. [In Japanese.]

1952c. On the plankton of Nakano-Umi in summer, 1948. The Journal of the Shimonoseki College of Fisheries 2(1): 48–53. [In Japanese.]

1953a. Some observations on the morphological characteristics especially on the reproductive organ of Copepoda, *Calanus darwini*. The Journal of the Shimonoseki College of Fisheries 3(3): 235–238. [In Japanese.]

1953b. Studies on the pelagic Copepoda from the Japan Sea. 1. On the genus *Euchaeta* Philippi, 1843. Bulletin of the Japanese Society of Scientific Fisheries 18(11): 613–617.

1956. Studies on the development and the systematics of Copepoda. The Journal of the Shimonoseki College of Fisheries 6(1): 1–90. [In Japanese.]

Chiba, T., A. Tsuruta, and H. Maéda.

1955. Report on zooplankton samples hauled by larva-net during the cruise of Bikini expedition, with special reference to copepods. The Journal of the Shimonoseki College of Fisheries 5(3): 189–213.

Dakin, W. J., and A. N. Colefax.

1940. The plankton of the Australian coastal waters off New South Wales. Pt. 1. Publications of the University of Sydney, Department of Zoology Monograph 1, p. 1–211.

Davis, C. C.

1949. Pelagic Copepoda of the northeastern Pacific Ocean. University of Washington Publications in Zoology. Vol. 14, 117 p.

Esterly, C. O.

1905. The pelagic Copepoda of the San Diego region. University of California Publications in Zoology 2(4): 113–233.

1906. Additions to the copepod fauna of the San Diego region. University of California Publications in Zoology 3(5): 53–92.

1911. Third report on the Copepoda of the San Diego region. University of California Publications in Zoology 6(14): 313–352.

1913. Fourth taxonomic report on the Copepoda of the San Diego region. University of California Publications in Zoology 11(10): 181–196.

1924. The free swimming Copepoda of San Francisco Bay. University of California Publications in Zoology 26(5): 81–129.

Farran, G. P.

1929. Crustacea. Part X. Copepoda. British Antarctic (*Terra Nova*) Expedition, 1910, Natural History Report, Zoology 8(3): 203–306.

1936. Copepoda. Great Barrier Reef Expedition 1928–29. Scientific Reports 5(3): 73–142.

Fleminger, A.

1956. Taxonomic and distributional studies on the epiplanktonic calanoid copepods (Crustacea) of the Gulf of Mexico. Doctoral Dissertation, Harvard University Library.

Fleminger, A., and T. E. Bowman.

1956. A new species of *Candacia* (Copepoda: Calanoida) from the western north Atlantic Ocean. Proceedings of the U.S. National Museum 106(3370): 331–337.

Fukase, S.

1957. Note on a variety of *Eucalanus subtenuis* Giesbrecht from the Japanese waters. Journal of the Oceanographical Society of Japan 13(1): 17–21.

Giesbrecht, W.

1888, 1889, 1891. Elenco dei copepodi pelagici raccolti dal tenente di vascello Gaetano Chierchia durante il viaggio della R. Corvetta *Vettor Pisani* negli anni 1882–1885 e dal tenente di vascello Francesco Orsini nel Mar Rosso, nel 1884. Atti della R. Accademia Nazionale dei Lincei Rendiconti, (4). Vol. 4, sem. 2 (1888): 284–287, 330–338. Vol. 5 (1889), sem. 1: 811–815; sem. 2: 24–29. Vol. 7 (1891), sem. 1: 474–481; sem. 2: 63–68, 276–282.

1892. Systematik und faunistik der pelagischen Copepoden des Golfes von Neapel. Fauna u. Flora des Golfes von Neapel u. d. angrenz Meeresabschnitte 19: 1–831.

1895. Die pelagischen Copepoden. Bulletin of the Museum of Comparative Zoology at Harvard College 25(12): 243–263.

1896. Ueber pelagische Copepoden des Rothen Meeres gesammelt vom marinestabsarzt Dr. Augustin Krämer. Zoologische Jahrbucher, Abt. Systematik. Vol. 9, p. 315–327.

Giesbrecht, W., and O. Schmeil.

1898. Copepoda I. Gymnoplea. Das Tierreich, Lief. 6, 169 p.

Gilmartin, M.

1958. Some observations on the lagoon plankton of Eniwetok Atoll. Pacific Science 12(4): 313–316.

Grice, G. D.

1959. A new species of *Haloptilus* (Copepoda: Calanoida) from equatorial and subtropical waters of the east-central Pacific Ocean. Journal of the Washington Academy of Sciences 49(6): 193–195.

Grice, G. D., and E. C. Jones.

1960. Two new species of *Candacia* (Copepoda: Calanoida) from the central Pacific with notes on two other species. Pacific Science 14(3): 280–291.

Heinrich, A. K.

1957a. The distribution of *Calanus tenuicornis* Dana and *Calanus lighti* Bowman in the north Pacific. Doklady Akademii Nauk S.S.S.R. 116 (4): 691–693 [In Russian.]

1957b. The vertical distribution of the plankton to the southeast from the Bonin Islands. Doklady Akademii Nauk S.S.S.R. 117(2): 321–324. [In Russian.]

1958a. The vertical distribution of copepods in the Kuroshio Current and the way they penetrate into the zone of mixing of subtropical and subarctic waters. Doklady Akademii Nauk S.S.S.R. 118(6): 1191–1193. [In Russian.]

1958b. On the feeding of copepods in the tropical region. Doklady Akademii Nauk S.S.S.R. 119 (5): 1028–1031. [In Russian.]

Hida, T., and J. E. King.

1955. Vertical distribution of zooplankton in the central equatorial Pacific, July–August 1952. U.S. Fish and Wildlife Service, Special Scientific Report—Fisheries No. 144, 22 p.

Honjo, K.

1952. Distribution of Copepoda in the adjacent sea of the Izu Islands during winter and spring. Bulletin of the Tokai Regional Fisheries Research Laboratory, No. 4, p. 1–5. [In Japanese.]

Honjo, K., H. Ohta, T. Kidachi, K. Umeda, and S. Kudoh.

1957. Distribution of Copepoda in the "Kuroshiro" area, south of Honshu, May, 1955. Records of Oceanographic Works in Japan, Special No. March 1957, p. 120–129.

Hure, J.

1955. Distribution annuelle verticale du zooplancton sur une station de l'Adriatique meridionale. Acta Adriatica Institut za Oceanografiju i Ribarstvo–Split fnr Jugoslavija 7(7): p. 1–72.

Japanese Hydrographic Office.

1956. Plankton observation. Equapac Expedition. Japanese Hydrographic Office. [Unpublished processed report.]

Johnson, M. W.

1942. Notes on Zooplankton. Records of Observations, Scripps Institution of Oceanography. Vol. 1, No. 1, Oceanographic Observations on the E. W. Scripps Cruises of 1938, p. 27–29.

1949. Zooplankton as an index of water exchange between Bikini Lagoon and the open sea. Transactions of the American Geophysical Union 30(2): 238–244.

1954. Bikini and nearby atolls. Pt. 2. Oceanography (biologic). Plankton of northern Marshall Islands. U.S. Geological Survey, Professional Paper F, p. 301–314.

King, J. E., T. S. Austin, and M. S. Doty.

1957. Preliminary report on expedition *Eastropic.* U.S. Fish and Wildlife Service, Special Scientific Report—Fisheries No. 201, 155 p.

Knauss, J. A.

1959. Direct current measurements at the equator–the Cromwell Current. International Oceanographic Congress, 31 August–12 September 1959. Preprints, American Association for the Advancement of Science, p. 515–516.

Knauss, J. A., and J. E. King.

1958. Observations of the Pacific equatorial undercurrent. Nature 182 (4635): 601–602.

Kokubo, S.

1950. The ecology of certain Copeda in Japan Sea, and Mutsu Bay. Bulletin of the Japanese Society of Scientific Fisheries 16(5): 215–220. [In Japanese.]

Legand, M.

1957. *Orsom III.* Résultats biologiques de l'expédition Equapac. Institut Français d'Océanie, Rapport Scientifique No. 1. [Processed report.]

Légaré, J. E. H.

1957. The qualitative and quantitative distribution of plankton in the Strait of Georgia in relation to certain oceanographic factors. Journal of the Fisheries Research Board of Canada 14(4): 551–552.

Lindberg, G. U.

1959. A list of the fauna of sea waters of the south Sakhalin and south Kurile Islands. Investigations of Far Eastern Seas. VI. Academy of Sciences of the U.S.S.R., p. 173–256. [In Russian.]

Lowe, C. W.

1936. Observations on some Pacific diatoms as the food of copepods and fishes. Journal of the Biological Board of Canada 3(1): 12–19.

McEwen, G. F., M. W. Johnson, and T. R. Folsom.

1954. A statistical analysis of the performance of the Folsom plankton sample splitter, based upon test observations. Archiv für Meteorologie, Geophysik und Bioklimatologie, Ser. A., 7: 502–527.

McMurrich, J. P.

1916. Notes on the plankton of the B. C. coast. Transactions of the Royal Society of Canada 10, Ser. 3, sect. 5:75–89.

Marukawa, H.

1921. Plankton list and some new species of Copepoda from the northern waters of Japan. Bulletin Institute of Oceanography No. 384.

Mori, T.

1930. An annotated list of the pelagic Copepoda from the S. W. part of the Japan Sea with descriptions of two new species. Zoological Magazine 41(487): 199–209. [In Japanese.]

1932. New copepods from southern Japan. Zoological Magazine, 44(523): 167–177. [In Japanese.]

1937. The pelagic Copepoda from the neighbouring waters of Japan. Tokyo. 150 p.

1942. Systematic studies of the plankton organisms occurring in Iwayama Bay, Palao. IV Copepoda from the Bay and adjacent waters. Palao Tropical Biological Station Studies, 2(3): 549–580.

Motoda, S., and M. Anraku.

1951. An observation on the vertical distribution of plankton at Ishikari Bay, Hokkaido. Journal of the Oceanographic Society of Japan 6(4): 194–201. [In Japanese.]

1952a. Observations on the plankton of Funka Bay, Hokkaido. I. Vertical distribution of plankton at the mouth of the bay in August 1950. Bulletin of the Hokkaido Region Fisheries Laboratory, No. 5, p. 17–20. [In Japanese.]

1952b. Plankton investigations (spring and summer, 1951). Report of the Deep Sea Fisheries of the Northern Japan Sea, No. 3, p. 71–76. [In Japanese.]

1954. Daily change of vertical distribution of plankton animals near western entrance to the Tsugaru Strait, Northern Japan. Bulletin of the

Faculty of Fisheries, Hokkkaido University 5(1): 15–19.

1955. Marine plankton copepods from the Hachijo Island, Idzu Islands, with special reference to their vertical distribution. Records of Oceanographic Works in Japan 2(1): 210–214.

Motoda, S., A. Iizuka, and M. Anraku.

1950. Plankton distribution to the northwest of Hokkaido in summer 1949. Report of the Deep Sea Fisheries of the Northern Japan Sea, No. 1, p. 78–109. [In Japanese.]

Nagaya, Y., Y. Komaki, T. Chiba, A. Tsuruta, and H. Maéda.

1955. Effects of artificial radioactivity on plankton. Publication of the Fishery Agency of Japan, p. 33–54. [In Japanese.]

Nakai, Z.

1952. On quantitative distribution of plankton reproduced in the northern Pacific. Tokai Regional Fisheries Laboratory, Special Publication No. 2, p. 1–6.

1955. The chemical composition, volume, weight, and size of the important marine plankton. Tokai Regional Fisheries Research Laboratory, Special Publication No. 5, p. 12–24.

Ponomareva, L. A.

1959. Some data on the zooplankton of the western coast of the south Sakhalin Island. Investigations of Far Eastern Seas. VI. Academy of Sciences of the U.S.S.R., p. 47–57. [In Russian.]

Rose, M.

1933. Copépodes pélagiques. Faune de France, 26: 1–374.

1934. Recherches complementaires sur les copépodes pélagiques de baie d'Alger. Bulletin de la Société d'histoire naturelle de l'Afrique du Nord 25(5): 145–148.

1942. Les Scolecithricidae (Copépodes pélagiques) de la Baie d'Alger. Annales de l'Institut Océanographique, n. s. 21, Pt. 3: 113–170.

1955. Quelques notes sur le plancton marin recueilli en 1953, par M. G. Ranson, dans la baie de Nhatrang-Canda (Viet Nam). Bull. du Muséum, 2e serie, vol. 27, No. 5.

Sars, G. O.

1903. Copepoda. Calanoida. Crustacea of Norway, Volume IV. 171 p.

1905. Listes preliminaires de Calanoides recueillis pendant les campagnes de S.A.S. le Prince Albert de Monaco avec diagnoses des genres et des espèces nouvelles. Bulletin du Musée Océanographique de Monaco, No. 26, 22 p.

Schmitt, W. L.

1939. Decapoda and other crustacea collected on the Presidential cruise of 1938. Smithsonian Miscellaneous Collections 98(6): 29 p.

Scott, A.

1909. The Copepoda of the *Siboga* expedition. Pt. 1. Free swimming, littoral and semi-parasitic Copepoda. Siboga-Expéditie Monographie 29a, p. 1–323.

Scott, T.

1894. Report on Entomostraca from the Gulf of Guinea. Transactions of the Linnean Society of London, series 2, Zoology. Vol. 6, Pt. 1, 161 p.

Scripps Institution of Oceanography.

1957. Data collected by Scripps Institution vessels on Equapac Expedition, August 1956. Scripps Institution of Oceanography Data Report, ref. 57–25. [Processed report.]

Sewell, R. B. S.

1929, 1932. The Copepoda of Indian Seas. Calanoida. Memoirs of the Indian Museum 10: 1–221 (1929), 223–407 (1932).

1947. The free swimming planktonic Copepoda. Systematic Account. *John Murray* Expedition 1933–34. Scientific Report 8(1): 1–303.

Shen, Chia-Jui, and Sye-O Bai.

1956. The Marine Copepoda from the spawning ground of *Pneumatophorus japonicus* (Houttuyn) off Chefoo, China. Acta Zoologica Sinica 8(2): 177–234. [In Chinese.]

Steuer, A.

1932. Copepoda 6: *Pleuromamma* Giesbr. 1898 der Deutschen Tiefsee-Expedition. Wissenschaftliche Ergebnisse der Deutschen Tiefsee-Expedition, 1898–1899, 24(1): 1–119.

Streets, T. H.

1877. Contribution to the natural history of the Hawaiian and Fanning Islands and lower California. Bulletin, U.S. National Museum, No. 7, p. 1–172.

Tanaka, O.

1935a. The Copepoda of Sagami Bay. Family Eucalanidae I. Suisan Gakkwai Ho (Tokyo) 6(3): 142–165. [In Japanese.]

1935b. The Copepods of Sagami Bay. Pt. II. The family Candaciidae. Suisan Gakkwai Ho (Tokyo) 6(4): 210–227. [In Japanese.]

1936. On some new species of Copepoda from Sagami Bay. Japanese Journal of Zoology 7(1): 31–36.

1937. Copepods from the deep water of Suruga Bay. Japanese Journal of Zoology 7(2): 251–271.

1953. The pelagic copepods of the Izu region. Records of Oceanographic Works in Japan 1(1): 126–137.

1956a. The pelagic copepods of the Izu Region, middle Japan. Systematic Account. I. Families Calanidae and Eucalanidae. Publications of the Seto Marine Biological Laboratory 5(2): 251–272.

1956b. The pelagic copepods of the Izu Region, middle Japan. Systematic Account. II. Families Paracalanidae and Pseudocalanidae. Publications of the Seto Marine Biological Laboratory 5(3): 367–406.

1957a. The pelagic copepods of the Izu Region, middle Japan. Systematic Account. III. Family Aetideidae (Part 1). Publications of the Seto Marine Biological Laboratory 6(1): 31–68.

1957b. The pelagic copepods of the Izu Region, middle Japan. Systematic Account. IV. Family Aetideidae (Pt. 2). Publications of the Seto Marine Biological Laboratory 6(2): 169–207.

1958. The pelagic copepods of the Izu Region, middle Japan. Systematic Account. V. Family Euchaetidae. Publications of the Seto Marine Biological Laboratory 6(3): 327–367.

TSURUTA, A., and T. CHIBA.

1954a. On the distribution of plankton at the fishing ground of salmons in the north Pacific Ocean, 1952. Journal of the Shimonoseki College of Fisheries 3(3): 239–245. [In Japanese.]

1954b. On the plankton at the fishing ground of tuna in the mid-Pacific Ocean. (1953.) Journal of the Shimonoseki College of Fisheries 3(3): 247–253. [In Japanese.]

VERVOORT, W.

1946. Biological results of the *Snellius* Expedition. XV. The bathypelagic Copepoda Calanoida of the *Snellius* Expedition. I. Families Calanidae, Eucalanidae, Paracalanidae, and Pseudocalanidae. Temminckia 8: 1–181.

1949. Some new and rare Copepoda Calanoida from east Indian Seas. Zoologische Verhandelingen, No. 5, 53 p.

1950. On the identity of *Onchocalanus nudipes* C. B. Wilson, 1942. Proceedings of the Section of Sciences, Koninklijke Nederlandse Akademie van Wetenschappen 53(1): 83–92.

1951. Plankton copepods from the Atlantic sector of the Antarctic. Verhandelingen der Koninklijke Nederlandse Akademie van Wetenschappen Afdeeling Natuurkunde, Sect. 2. Vol. 47 (no. 4): 1–156.

1952. Copepoda. Sub-order Calanoida. Family Aetideidae, Genus *Euchirella*. Fiches d'Identification du Zooplancton 47. Conseil Permanent International pour l'Exploration de la Mer.

1957. Copepods from Antarctic and sub-Antarctic plankton samples. B.A.N.Z. Antarctic Research Expedition 1929–1931. Reports, Ser. B (Zoology and Botany), 160 p.

WILSON, C. B.

1942. The copepods of the plankton collected during the last cruise of the *Carnegie*. Carnegie Institution of Washington Publication No. 536, 237 p.

1950. Copepods gathered by the U.S. Fisheries steamer *Albatross* from 1887 to 1909, chiefly in the Pacific Ocean. U.S. National Museum Bulletin 100, 14(4): 141–441.

WOLFENDEN, R. N.

1905. Notes on the collection of Copepoda. The Fauna and Geography of the Maldive and Laccadive Archipelagoes. Vol. 2. Suppl. 1: 989–1040.

YAMADA, T.

1933a. On the distribution of the temperate plankton in the western part of the Korean Strait. Bulletin of the Japanese Society of Scientific Fisheries 1(6): 281–286. [In Japanese.]

1933b. Report on the distribution of the plankton in the neighboring seas of Tyosen in June 1932. Annual Report of the Hydrographic Observatory of the Fishery Experiment Station. Government General of Tyosen, No. 7. Appendix. [In Japanese.]

YAMAZI, I.

1950. Plankton investigations in inlet waters of Japan. I. Introductory notes and the plankton of Akkeshi Bay, Hanasaki Inlet and Nemuro Harbour. Publications of the Seto Marine Biological Laboratory 1(3): 93–113.

1951. Plankton investigations in inlet waters of Japan. II. The plankton of Hakodate Harbour and Yoichi Inlet in Hokkaido. Publications of the Seto Marine Biological Laboratory 1(4): 185–194.

1952a. Plankton investigations in inlet waters of Japan. III. The plankton of Imari Bay in Kyusyu. Publications of the Seto Marine Biological Laboratory 2(2): 289–304.

1952b. Plankton investigations in inlet waters of Japan. IV. The plankton of Nagasaki Bay and Nagasaki Harbour in Kyusyu. Publications of the Seto Marine Biological Laboratory 2(2): 305–318.

1952c. Plankton investigations in inlet waters of Japan. V. The plankton of Hiroshima Bay in the Seto-Naikai (Inland Sea). Publications of the Seto Marine Biological Laboratory 2(2): 319–330.

1953a. Plankton investigations in inlet waters of Japan. VII. The plankton collected during the cruises to the new Yamato Bank in the Japan Sea. Publications of the Seto Marine Biological Laboratory 3(1): 75–108.

1953b. Plankton investigations in inlet waters of Japan. IX. The plankton of Onagawa Bay on the eastern coast of Tôhoku district. Publications of the Seto Marine Biological Laboratory 3(2): 173–187.

1953c. Plankton investigations in inlet waters of Japan. X. The plankton of Kamaisi Bay on the eastern coast of Tôhoku district. Publications of the Seto Marine Biological Laboratory 3(2): 189–204.

1954a. Plankton investigations in inlet waters of Japan. XI. The plankton of Kozima Bay in the Seto-Naikai (Inland Sea). Publications of the Seto Marine Biological Laboratory 3(3): 399–421.

1954b. Plankton investigations in inlet waters of Japan. XII. Plankton of Miyako Bay on the eastern coast of Tôhoku district. Publications of the Seto Marine Biological Laboratory 3(3): 423–441.

1954c. Plankton investigations in inlet waters of Japan. XIII. The plankton of Obama Bay on the Japan Sea coast. Publications of the Seto Marine Biological Laboratory 4(1): 103–114.

1954d. Plankton investigations in inlet waters of Japan. XIV. The plankton of Turuga Bay on the Japan Sea coast. Publications of the Seto Marine Biological Laboratory 4(1): 115–126.

1954e. Plankton investigations in inlet waters of Japan. XV. The plankton of Yosa–Naikai and Kumihama Bay, enclosed bays on the Japan Sea coast. Publications of the Seto Marine Biological Laboratory 4(1): 127–145.

1955a. Plankton investigations in inlet waters of Japan. VIII. The plankton of Miyazu Bay in relation to the water movement. Publications of the Seto Marine Biological Laboratory 4(2–3): 269–284.

1955b. Plankton investigations in inlet waters of Japan. XVI. The plankton of Tôkyô Bay in relation to the water movement. Publications of the Seto Marine Biological Laboratory 4(2–3): 285–309.

1955c. Plankton investigations in inlet waters of Japan. XVII. Seasonal succession of zooplankton in the inner area of Tanabe Bay from June to October 1954. Publications of the Seto Marine Biological Laboratory 4(2–3): 311–320.

1957. Plankton investigations in inlet waters of Japan. XX. Diurnal change of plankton animals at an innermost station in Wakayama Harbor. Publications of the Seto Marine Biological Laboratory 6(2): 209–224.

1958a. Preliminary check-list of plankton organisms found in Tanabe Bay and its environs. Publications of the Seto Marine Biological Laboratory 7(1): 111–163.

1958b. A study on the productivity of the Tanabe Bay. Pt. I, IV. On some plankton indicating the water exchange in the Tanabe Bay. Records of Oceanographic Works in Japan Special Publication No. 2, p. 25–35.

Yamazi, I., and T. Horibata.

1955. Plankton investigations in inlet waters of Japan. XVIII. Seasonal succession of plankton in Taizi Bay in the years 1951–1953. Publications of the Seto Marine Biological Laboratory 4(2–3): 321–336.

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ABUNDANCE AND DISTRIBUTION OF EGGS AND LARVAE AND SURVIVAL OF LARVAE OF JACK MACKEREL (*TRACHURUS SYMMETRICUS*)

By DAVID A. FARRIS

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ABSTRACT

Distribution and abundance of eggs and larvae of the jack mackerel, *Trachurus symmetricus* (Ayres), and survival of the larvae are described, utilizing quantitative data collected on monthly cruises of the California Cooperative Oceanic Fisheries Investigations during 1951–54.

Spawning in the period 1951–1954 occurred from Washington to Magdalena Bay, Baja California. In each of the 4 years it began in February and ceased by October. The peak month of spawning was March in 1951 and May in 1952, 1953, and 1954. About 30 percent of the spawning occurred during the peak month. Estimates of egg abundance varied by less than a factor of 2 during the 4 years studied.

The effect of temperature on the rate of development of eggs was investigated. Regression statistics are given for the developmental rate. Reliability of the regression was checked by direct observation of developing eggs at controlled temperatures.

The annual estimates of survival for 1952, 1953, and 1954 indicate a reasonably constant survival of month-old jack mackerel larvae in these years.

The growth rate of jack mackerel larvae was approximated from data derived by direct observation of developing jack mackerel larvae under laboratory conditions and was described by two successive logarithmic growth curves. The second curve originates at yolk sac absorption and has the lesser slope.

Survival data may be broken into two periods: the first period, concurrent with the fast growth period, is characterized by poor survival and may be the critical period; in the second, survival is much better and growth much slower.

ABUNDANCE AND DISTRIBUTION OF EGGS AND LARVAE AND SURVIVAL OF LARVAE OF JACK MACKEREL (*TRACHURUS SYMMETRICUS*)

By David A. Farris, *Fishery Research Biologist*
Bureau of Commercial Fisheries

The purposes of this study are to delimit both spatially and temporally the spawning of the jack mackerel, *Trachurus symmetricus* (Ayres) 1885, and to estimate the abundance of the eggs and the survival rate of the larvae. Quantitative data collected on monthly cruises of the California Cooperative Oceanic Fisheries Investigations, 1951 through 1954, are utilized in the study.

Data derived from the study of eggs and larvae may give insight into the present abundance and future fluctuations of the adult population, and estimates of larval mortality may aid in predicting future recruitment to the fishery. With knowledge of the fecundity, estimates of egg abundance may be used to ascertain the present size of the adult population. These data may also be compared with physical, chemical, and other biological data gathered by the California Cooperative Oceanic Fisheries Investigations.

To accomplish the stated purposes of this study, the following information was needed:

1. Boundaries of the area occupied by developing eggs and larvae.
2. Seasonal distribution of the eggs and larvae within those boundaries.
3. Quantitative depth distribution of the eggs and larvae.
4. Relation between temperature and rate of development of eggs and larvae.

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REVIEW OF THE FISHERY

The carangids most commonly found in the area surveyed by the California Cooperative Oceanic Fisheries Investigations are listed by Barnhart (1936) and Fowler (1944). The family is largely tropical or subtropical in its distribution, *Trachurus symmetricus* being a notable exception. Only three members of the family are taken in any numbers by the California Cooperative Oceanic Fisheries Investigations: yellowtail, *Seriola dorsalis* Gill; Mexican scad, *Decapterus hypodus* Gill; and jack mackerel, *Trachurus symmetricus* (Ayres). The larvae of all three species are known, so that identification is possible. The yellowtail and jack mackerel are the only carangids of any economic importance in the area (Clothier and Greenhood, 1956).

Well over 80 percent of the jack mackerel fishery is located in waters off southern California (i.e., from Point Conception to the Mexican border). In some years 99 percent of the catch is made in this region. Less than 1 percent of the total catch is taken in waters as far north as Eureka, California (i.e., Point Conception to Eureka).

Before 1947 the jack mackerel catch never exceeded 7,550 tons (Roedel, 1949: p. 31–32), and since then it has not fallen below that figure. During 3 years, 1947, 1950, and 1952, the catch exceeded 62,500 tons. The fluctuations of the jack mackerel catch more or less complement fluctuations in the sardine catch (Clothier and Greenhood,

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Note.—The author's official address is San Diego State College, San Diego, California.

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[1] Presently the Bureau of Commercial Fisheries Biological Laboratory, La Jolla, Calif.

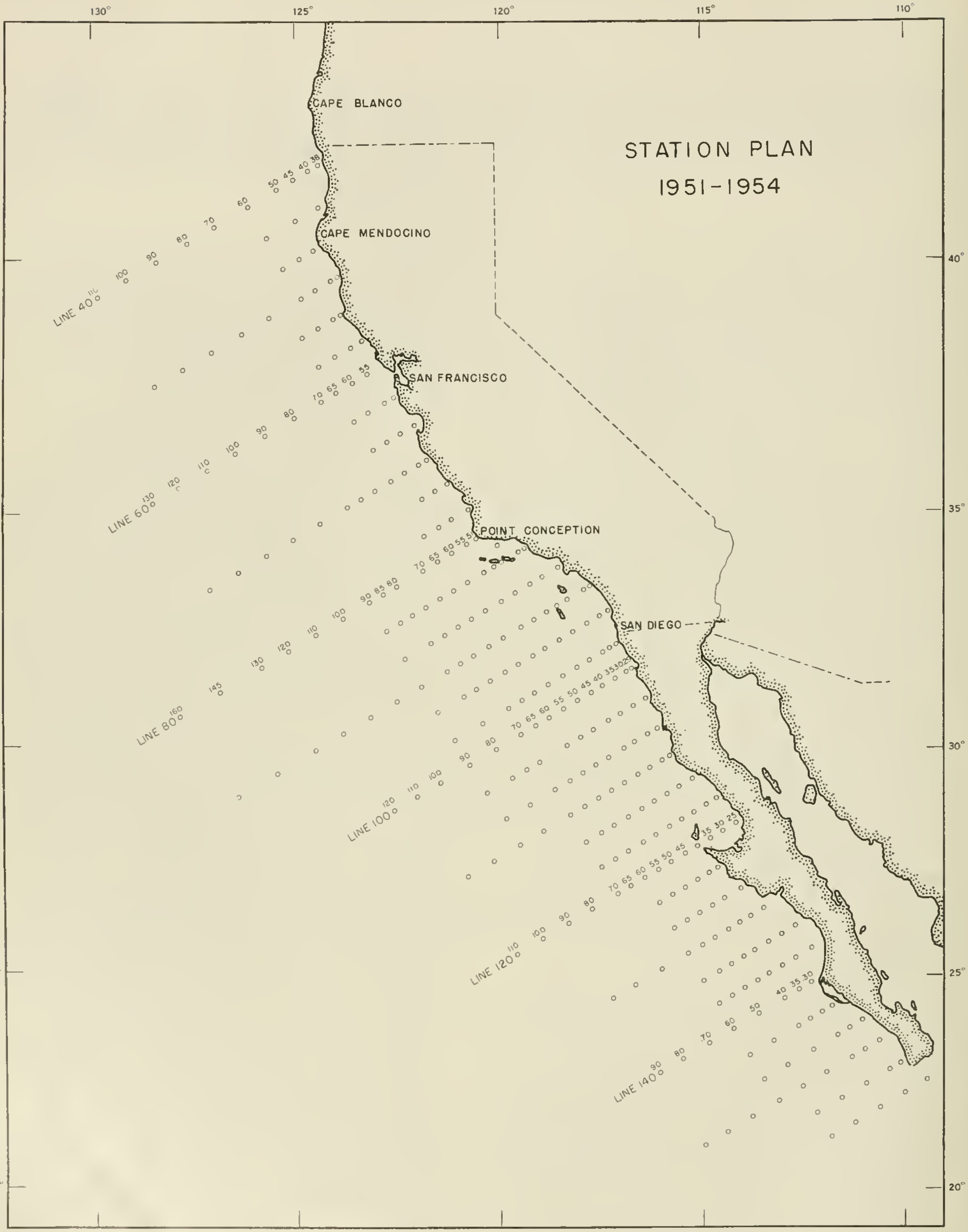

FIGURE 1.—Chart of stations occupied by the California Cooperative Oceanic Fisheries Investigations 1951–1954.

1956: p. 8 and 12). The catch fluctuations since 1947 arise primarily from three causes: (1) Availability of sardines and Pacific mackerel, (2) fluctuations in demand for canned jack mackerel, and (3) availability of the jack mackerel. Since jack mackerel are packed as "substitute sardines," catch data do not necessarily reflect the size of the adult population. Eventual independence of the industry is assured, however, by the world's increasing need for cheap protein and by technological advances in the packing of this species.

Jack mackerel are taken with a variety of gear; however, more than 99 percent are taken with purse seines and lampara nets. The operation of this gear is described by Scofield (1951). Some jack mackerel are taken by sport fishermen using live bait. In 1953, the sport catch was unusually large, nearly 200,000 fish being taken (Fitch, 1956: p. 27). However, this catch amounts to less than 2 percent of the commercial catch.

Except for a minor amount used in the fresh-fish market, the commercial catch is used for canning. Jack mackerel are principally packed sardine style, usually in tall, 1 pound cans. A small part of the catch is packed in other ways.

To date, the catch of jack mackerel has not undergone any sustained decline. Therefore, all the previously mentioned data take on an added significance when one considers that many fishery investigations are initiated after the industry has experienced a decline in the number of catchable fish (Walford, 1948). By noting the variations in the strength of spawning, stock size, mortality, et cetera, now while fishing mortality is relatively low, future observations under conditions of higher fishing mortality should permit the assessment of the effects of man on the population size of the jack mackerel.

METHODS OF COLLECTING DATA

Since this study of jack mackerel constitutes but part of a larger and more comprehensive study of the ecology of pelagic fishes off the coast of California, the methods used are those originated by the Bureau of Commercial Fisheries Biological Laboratory at La Jolla and adopted by the staffs of the California Cooperative Oceanic Fisheries Investigations. These methods have been planned to maximize the amount of information obtainable from this ecological province.

The methods used in collecting and processing these data, with a summary of the previous year's work are found in reports of the California Marine Research Committee, the sponsoring organization of the California Cooperative Oceanic Fisheries Investigations, for 1950, 1952, 1953, 1955, and 1956. More detailed explanations are given by Ahlstrom (1948 and 1953), and in the following discussion.

The station pattern and numbering system are described in Station Positions of the California Cooperative Sardine Research Program, prepared by the Scripps Institution of Oceanography and the U.S. Fish and Wildlife Service (1952). The stations laid out in lines occupied during the period 1951–54 are shown in figure 1. The exact location of each station (at each occupancy) during 1951–54 is given by Staff, South Pacific Fishery Investigations (1952, 1953, 1954, and 1955). A plankton-net tow (Ahlstrom, 1953), Nansen bottle cast, and bathythermograph cast are made at each station. Temperature data are obtained from the reversing thermometers on Nansen bottles and from bathythermograms. The obliquely hauled plankton net is retrieved from a depth of approximately 140 meters (200 meters of wire out) at an average rate of 20 meters of wire per minute. The angle from the vertical of the towing wire is kept as close as possible to 45 degrees. A current meter placed in the mouth of the net measures the volume of water strained. The sample obtained is preserved in its entirety in a buffered formalin solution, and these preserved samples are subsequently examined for fish eggs and larvae. The numbers of jack mackerel larvae and localities in which they were taken during 1952–54 are given in Ahlstrom (1954a) and Ahlstrom and Kramer (1955, 1956). The numbers of jack mackerel eggs and localities in which they were taken in 1951–54 are given by Farris (1958).

ESTIMATING EGG ABUNDANCE

The method used to estimate egg abundance has been described in detail by Sette and Ahlstrom (1948) and Ahlstrom (1954b). The monthly estimates of egg abundance are obtained from the relation—

$$C_M = \sum_{i=1}^{n} c_i w_i t_i$$

where

C_M = the monthly estimate of egg abundance

n = the number of stations considered
c_i = the average number of eggs spawned per day at the ith station[2]
w_i = the weighting factor for space in standard area (i.e., units of 10 m^2 of sea surface)
t_i = the time factor which is equal to one-half the time from the preceding occupancy of the station plus one-half the time to the succeeding occupancy.

An annual estimate of abundance is obtained by summing the monthly estimates for the entire year.

The eggs are identified and the number belonging to each species is recorded by station. The count for each station is adjusted so that all results are expressed as the number of eggs under a standard area which is 10 square meters of sea surface (Ahlstrom, 1953). This standardized haul value (c'_i) is the product of the raw count times a standard haul factor, which is derived for each haul by dividing 10 by the average volume of water strained per meter of depth for the entire water column.

EFFECT OF TEMPERATURE ON LENGTH OF INCUBATION PERIOD

The length of the incubation period (d_i) is dependent on temperature of the water mass in which the eggs are developing, and may be predicted if the temperature coefficient for the rate of development is known.

The effect of temperature on the rate of development of jack mackerel eggs has been derived by two methods. In the first method, the eggs were taken from the sea shortly after they had been spawned, placed in a fish egg incubator (see appendix A) and observed at 4-hour intervals until they hatched. The temperature of the water in the incubator was maintained at about 14° C., the temperature of the sea water from which the eggs were collected. The observed hatching time was 108.5 hours. This experiment was repeated 1 year later at 15° C., with an observed hatching time of 84 hours.

The second method, which is indirect, was developed by Ahlstrom (1943) for the Pacific sardine and was also successfully used by Gamulin and Hure (1955) for sardines in the Mediterranean Sea. A series of arbitrarily chosen but precisely defined morphological stages is selected. Such a series of stages is described for jack mackerel in appendix B. The jack mackerel eggs from station samples are separated into stages and counted (Farris, 1958: table 2, p. 7–11).

Several successive days of spawning are indicated by the stage frequency modes present in each sample. A mode is interpreted as representing 1 day's spawn, inasmuch as spawning is limited to a short period each night and the modes represent stages separable by a day as determined from incubation experiments.

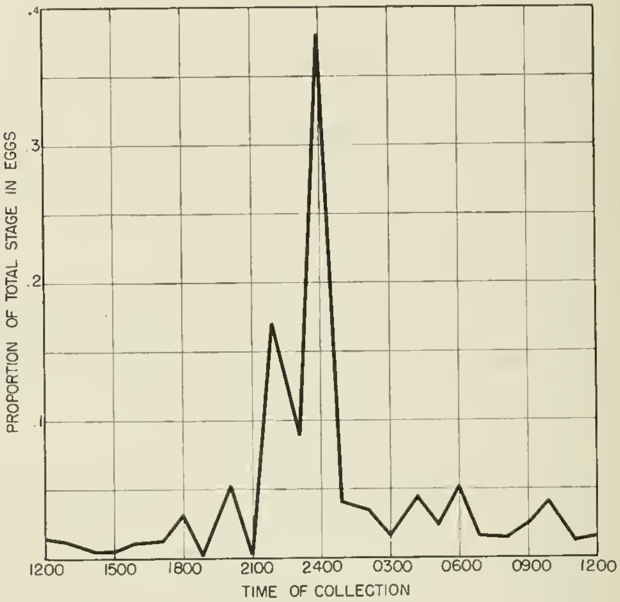

Figure 2.—Stage-I jack mackerel eggs collected in 1951 by hour of collection. All stage-I eggs collected at a particular hour are expressed as a proportion of the total stage-I eggs for the year.

The time of day at which spawning takes place was determined by plotting the relative abundance of precleavage eggs (stage I) against time of collection (fig. 2). The time the samples were collected is given in a report of the South Pacific Fishery Investigations (1952). These data showed the time of maximum spawning for jack mackerel was approximately midnight.

The age of the earliest stage is computed by subtracting the hour of collection from midnight. The age of the second mode is estimated by adding 24 hours to the age of the first mode, and the age of subsequent modes is determined in the same manner.

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[2] c_i is derived as follows: $c_i = c'_i/d_i$ where c'_i = the standard number of eggs at the ith station; d_i = the time interval in days from spawning to hatching.

Temperature data for the stations were supplied by the Scripps Institution of Oceanography. If the temperatures within the upper 30 meters of water did not vary by more than 0.1° C., the data from the station were used.

The effect of temperature on rate of development was shown by a regression of log hours of development against temperature for each stage.

Y=hours of development
X=temperature °C.
$\text{Log } Y=a+bX$

Separate regressions were made for three stages (table 1) so that the regression statistics might be compared. If a relation exists between rate of development and temperature, the slopes for the three regressions should be about the same. The Y-intercepts were not compared, since the lines are almost parallel and occur at different levels; the intercepts, as one would expect, are different.

TABLE 1.—*Temperature regression coefficients for the rate of development of jack mackerel eggs*

Statistic	Stage		
	V	VIII	IX
a	2.996	3.047	3.257
b	−0.093	−0.088	−0.088
$\overline{X}$ (temperature °C.)	15.71	15.40	15.40
$\overline{Y}$ (log hours)	1.580	1.690	1.891

The close correspondence of the slopes for the three regressions indicates a uniform relation between developmental rate and temperature. By using the graph of the regression for the oldest stage (stage IX), the incubation period to the closest day could be predicted directly (fig. 3). This regression was used in determining the number of whole days elapsing in the egg stage (d_i) as mentioned above.

The incubation period (in hours) as predicted by the regression for stage-IX eggs was compared with the incubation period actually observed under conditions of controlled temperature (see p. 250). The close agreement between prediction and observation is shown in the following table:

Temperature (°C.)	Predicted hours	Observed hours
14	106	108.5
15	86.5	84

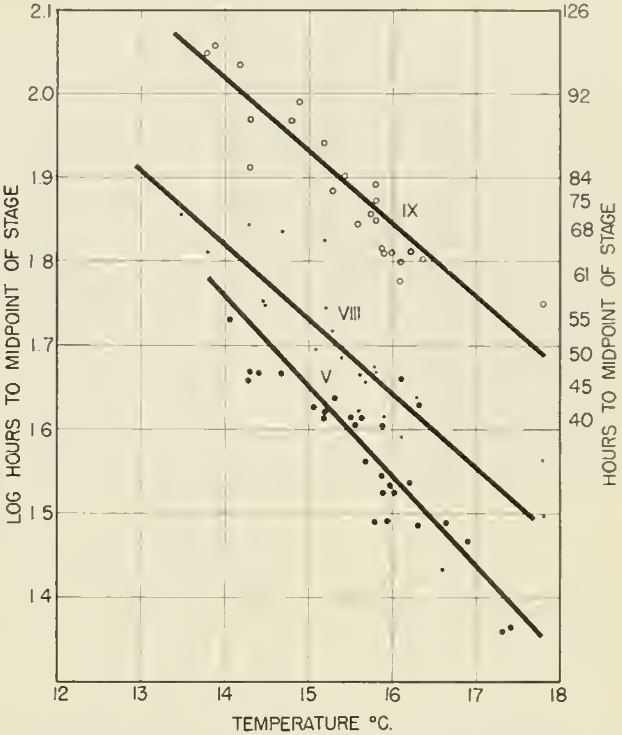

FIGURE 3.—Relation between temperature and rate of development for three stages of jack mackerel eggs.

The close agreement between incubation period predicted and actually observed lent confidence to the reliability of the indirect method.

The temperature-dependent incubation period (d_i) is used to compute the average number of eggs spawned per day at the ith station (c_i) in the following manner.

The standard number of eggs at the ith station (c'_i) is divided by d_i.

After computing the estimate of the average number of eggs spawned per day at the ith station of 10 square meters, the number of eggs is integrated over space to the surrounding stations by an area factor (w_i). The sample is then weighted on the basis of the area it represents. The boundaries of an area are formed by the perpendicular bisectors of lines drawn to the stations immediately surrounding the one under consideration.

The time factor (t_i) is derived by taking the number of days from the previous occupancy of the station to the occupancy of the station immediately succeeding the one under consideration and dividing by 2. The products ($c_iw_it_i$) are summed for the month to give an estimate of total monthly egg abundance (C_M).

ESTIMATES OF EGG ABUNDANCE AND SEASONAL-REGIONAL DISTRIBUTION OF SPAWNERS

Using the method of Ahlstrom (1954b) previously described, the monthly estimates by region were obtained for the 4-year period, 1951–54 (tables 2–5). Spawning does not occur uniformly over the area throughout the spawning season and the seasonal-regional variation is discussed in the following section.

The estimates of egg abundance revealed that during this 4-year period, the highest annual estimate (1951) was less than twice that of the lowest (1954). Furthermore, no trend was apparent from 1951 through 1954. Spawning averaged 666 trillion eggs per year, with a range of 873 trillion to 462 trillion.

The seasonal distribution of spawners was inferred from the monthly estimates of egg abundance and the number of eggs spawned per month expressed as a percent of the annual total for each year. Although the percentages have been carried to hundredths, no statistical significance should be attached to these postdecimal places which merely serve to indicate trace amounts of spawning. These figures are given in the last row in tables 2 through 5.

TABLE 2.—*Estimated number (in billions) of jack mackerel eggs in survey area, 1951*

[Cruise numbers in parentheses. No eggs taken during cruises 5101 and 5110 to 5112]

	Feb. (5102)	Mar. (5103)	Apr. (5104)	May (5105)	June (5106)	July (5107)	Aug. (5108)	Sept. (5109)	Annual total	Percent of total for all areas
North of Point Conception:										
Lines 40–57	----------	----------	----------	----------	----------	1, 365	2, 907	----------	4, 272	----------
60–77	----------	----------	8, 616	8, 099	62, 487	22, 235	206	0	101, 643	----------
Total and percent	----------	----------	8, 616	8, 099	62, 487	23, 600	3, 113	0	105, 915	12. 13
Southern California:										
Line 80	44, 060	50, 497	2, 476	47	7, 915	1, 228	53	12	106, 288	----------
83	0	----------	0	3, 863	4, 932	----------	----------	0	8, 795	----------
85	----------	40, 344	----------	----------	----------	0	890	0	41, 234	----------
87	0	----------	9, 706	30, 784	1, 973	----------	0	----------	42, 463	----------
90	2, 829	48, 338	33, 804	22, 298	13, 712	10, 412	7, 334	15	138, 742	----------
93	8, 930	30, 972	18, 977	9, 568	3, 107	2, 559	2, 071	0	76, 184	----------
Total and percent	55, 819	170, 151	64, 963	66, 560	31, 639	14, 199	10, 348	27	413, 706	47. 40
Northern Baja California:										
Line 97	6, 379	10, 564	15, 014	6, 486	12, 964	7, 421	1, 442	16	60, 286	----------
100	1, 970	7, 469	19, 735	18, 484	3, 761	21, 484	907	0	73, 810	----------
103	----------	14, 487	16, 490	3, 614	3, 708	----------	----------	8	38, 307	----------
105	0	----------	----------	----------	----------	----------	307	----------	307	----------
107	----------	11, 282	6, 152	7, 348	2, 433	----------	----------	0	27, 215	----------
Total and percent	8, 349	43, 802	57, 391	35, 932	22, 866	28, 905	2, 656	24	199, 925	22. 91
Upper central Baja California:										
Line 110	0	20, 092	19, 439	7, 263	8, 754	890	424	0	56, 862	----------
113	0	17, 053	6, 756	3, 746	10, 209	----------	----------	----------	37, 764	----------
115	----------	----------	----------	----------	----------	----------	445	0	445	----------
117	0	20, 430	8, 530	3, 248	256	----------	----------	----------	32, 464	----------
120	0	291	4, 781	2, 318	14, 993	341	115	0	22, 839	----------
Total and percent	0	57, 866	39, 506	16, 575	34, 212	1, 231	984	0	150, 374	17. 23
Lower central Baja California:										
Line 123	0	42	560	204	213	18	3	0	1, 040	----------
127	0	42	30	41	40	0	0	0	153	----------
130	0	63	451	101	0	0	0	0	615	----------
133	0	28	369	430	0	16	0	0	843	----------
137	0	0	0	49	0	0	0	0	49	----------
Total and percent	0	175	1, 410	825	253	34	3	0	2, 700	. 31
Southern Baja California:										
Line 140	----------	165	----------	----------	0	----------	----------	0	165	----------
143	----------	39	----------	----------	0	----------	----------	0	39	----------
147	----------	0	----------	----------	0	----------	----------	0	0	----------
150	----------	0	----------	----------	0	----------	----------	0	0	----------
Total and percent	----------	204	----------	----------	0	----------	----------	0	204	. 02
Grand total	64, 168	272, 198	171, 886	127, 991	151, 457	67, 969	17, 104	51	872, 824	----------
Percent [1]	7. 35	31. 19	19. 69	14. 66	17. 35	7. 79	1. 96	0. 01	100. 00	----------

[1] Hundredths of a percent are used so that trace amounts of spawning may be indicated (see text above).

The regional (north-south) distribution of spawning fish was inferred from the regional distribution of eggs. The number of eggs found in a region was expressed as a percent of the total for all regions (i.e., annual total). These figures are given in the last column in tables 2 through 5. The lines comprising each region are as follows:

Region	Area	Lines
1	Northern California	40–77
2	Southern California	80–93
3	Northern Baja California	97–107
4	Upper central Baja California	110–120
5	Lower central Baja California	123–137
6	Southern Baja California	140–157

A slightly different approach was used to elucidate the offshore-inshore distribution. Unlike the preceding section, only selected stations on selected lines were used, because the selected data were more quickly and easily handled, and because these particular selected stations had the most regular coverage, having been occupied almost every month throughout the 4 years studied.

Only those lines and stations that are multiples of 10 were used (e.g., lines 40, 50, and 60, but not 63, 67, or 73, and stations 40, 50, and 60, but not 45, 55, or 65), except for the most inshore stations. The standardized numbers of eggs

TABLE 3.—*Estimated number (in billions) of jack mackerel eggs in survey area, 1952*

[Cruise numbers in parentheses. No eggs taken during cruises 5210 and 5211]

	Jan. (5201)	Feb. (5202)	Mar. (5203)	Apr. (5204)	May (5205)	June (5206)	July (5207)	Aug. (5208)	Sept. (5209)	Annual total	Percent of total for all areas
North of Point Conception:											
Lines 40–57	---	---	---	---	---	0	49	---	---	49	---
60–77	---	---	---	0	0	5, 278	9, 541	817	0	15, 636	---
Total and percent	---	---	---	0	0	5, 278	9, 590	817	0	15, 685	2. 64
Southern California:											
Line 80	0	161	1, 993	0	2, 769	22, 624	3, 262	793	0	31, 602	---
83	---	---	---	107	6, 789	9, 290	---	---	---	16, 186	---
85	0	0	0	---	---	---	3, 108	0	27	3, 135	---
87	---	---	---	982	30, 880	4, 855	---	---	---	36, 717	---
90	0	7, 625	54, 153	3, 075	30, 302	20, 144	2, 013	3, 034	2, 262	122, 608	---
93	0	0	905	11, 713	9, 727	2, 944	8, 293	3, 001	109	36, 692	---
Total and percent	0	7, 786	57, 051	15, 877	80, 467	59, 857	16, 676	6, 828	2, 398	246, 940	41. 64
Northern Baja California:											
Line 97	33	1, 631	1, 691	34, 173	12, 380	8, 632	22, 058	1, 368	1, 600	83, 566	---
100	1, 813	11, 532	12, 735	26, 325	10, 821	4, 440	4, 839	0	127	72, 632	---
103	---	---	---	10, 914	24, 782	1, 428	---	27	8	37, 159	---
105	173	29, 562	1, 278	---	---	---	7, 475	---	---	38, 488	---
107	---	---	---	8, 899	12, 323	4, 323	---	15	13	25, 573	---
Total and percent	2, 019	42, 725	15, 704	80, 311	60, 306	18, 823	34, 372	1, 410	1, 748	257, 418	43. 40
Upper central Baja California:											
Line 110	0	0	63	18, 950	26, 376	4, 877	751	0	0	51, 017	---
113	---	0	325	1, 350	1, 944	2, 672	98	0	0	6, 389	---
115	0	---	---	---	---	---	---	---	---	0	---
117	---	0	61	132	539	2, 841	140	0	0	3, 713	---
120	0	0	1, 313	1, 777	4, 145	523	0	25	0	7, 783	---
Total and percent	0	0	1, 762	22, 209	33, 004	10, 913	989	25	0	68, 902	11. 63
Lower central Baja California:											
Line 123	0	0	1, 300	527	1, 978	239	0	0	0	4, 044	---
127	0	0	0	0	0	0	0	0	0	0	---
130	0	0	0	93	0	0	0	0	0	93	---
133	0	0	0	0	0	0	0	0	0	0	---
137	0	0	0	0	0	0	0	0	0	0	---
Total and percent	0	0	1, 300	620	1, 978	239	0	0	0	4, 137	. 69
Southern Baja California:											
Line 140	---	0	---	---	---	---	---	---	---	0	---
143	---	0	---	---	---	---	---	---	---	0	---
147	---	0	---	---	---	---	---	---	---	0	---
150	---	0	---	---	---	---	---	---	---	0	---
Total and percent	---	0	---	---	---	---	---	---	---	0	. 00
Grand total	2, 019	50, 511	75, 817	119, 017	175, 755	95, 110	61, 627	9, 080	4, 146	593, 082	---
Percent[1]	0. 34	8. 52	12. 78	20. 07	29. 63	16. 04	10. 39	1. 53	0. 70	100. 0	---

[1] Hundredths of a percent are used so that trace amounts of spawning may be indicated (see p. 252).

(instead of estimates of abundance) for these selected lines and stations were summed by 2-month intervals from February to July. The bimonthly totals for the lines were divided by the bimonthly totals for the entire area to give the bimonthly percentage of eggs found on the line. To estimate the offshore-inshore movements, stations 100 and seaward (offshore) were grouped together, stations 70–90 (intermediate) were grouped together, and stations 60-shore (inshore) were grouped together for each line. The station groups were summed bimonthly and the percentage of the bimonthly total for each of the three station groups was computed (tables 6, 7, 8, and 9). Table 10 presents a comparison of the estimates of relative regional abundance obtained from the standardized numbers of eggs at selected stations on selected lines and the regional distribution based on estimates of abundance using all data. Since the north-south regional distribution indicated by the selected data agreed with the north-south distribution indicated by all the data, no distortion was anticipated in using the selected data to reveal the offshore-inshore distribution.

TABLE 4.—*Estimated number (in billions) of jack mackerel eggs in survey area, 1953*

[Cruise numbers in parentheses. No eggs taken during cruises 5301, 5309, 5311, and 5312]

	Feb. (5302)	Mar. (5303)	Apr. (5304)	May (5305)	June (5306)	July (5307)	Aug. (5308)	Oct. (5310)	Annual total	Percent of total for all areas
North of Point Conception:										
Lines 40-57	----------	----------	----------	----------	----------	----------	----------	----------	----------	----------
60-77	----------	----------	12	0	6,075	1,947	1,619	----------	9,653	----------
Total and percent	----------	----------	12	0	6,075	1,947	1,619	----------	9,653	1.31
Southern California:										
Line 80	0	0	3,783	22,633	3,774	5,570	288	----------	36,048	----------
83	0	0	0	2,835	5,639	5,402	0	0	13,876	----------
85	0	0	0	152	590	3,252	18	----------	4,012	----------
87	0	0	0	12,813	3,285	1,769	55	----------	17,922	----------
90	0	0	5,512	60,199	1,241	7,016	378	47	74,393	----------
93	0	0	1,378	14,006	12,776	10,588	91	5	38,844	----------
Total and percent	0	0	10,673	112,638	27,305	33,597	830	52	185,095	25.14
Northern Baja California:										
Line 97	0	0	4,327	19,550	36,880	4,556	602	0	65,915	----------
100	14,348	4,508	2,700	5,664	14,660	8,939	1,232	181	52,232	----------
103	----------	----------	5,722	21,840	16,905	4,601	519	0	49,587	----------
105	2,196	70,331	----------	----------	----------	----------	----------	----------	72,527	----------
107	----------	----------	66,907	19,528	14,200	10,606	2,015	0	113,256	----------
Total and percent	16,544	74,839	79,656	66,582	82,645	28,702	4,368	181	353,517	48.02
Upper central Baja California:										
Line 110	9,585	27,732	59,051	5,847	1,228	2,250	1,122	0	106,815	----------
113	5,671	738	17,658	1,376	3,412	721	0	0	29,576	----------
115	----------	----------	----------	----------	----------	----------	----------	----------	----------	----------
117	4,239	1,964	7,505	5,090	2,324	231	0	0	21,353	----------
120	1,743	0	3,779	12,936	247	124	0	0	18,829	----------
Total and percent	21,238	30,434	87,993	25,249	7,211	3,326	1,122	0	176,573	23.99
Lower central Baja California:										
Line 123	0	0	0	6,701	81	0	0	0	6,782	----------
127	0	0	0	1,974	1,022	0	0	0	2,996	----------
130	0	0	0	1,327	140	0	0	0	1,467	----------
133	0	0	0	0	41	0	0	0	41	----------
137	0	0	0	0	8	0	0	0	8	----------
Total and percent	0	0	0	10,002	1,292	0	0	0	11,294	1.53
Southern Baja California:										
Line 140	----------	----------	----------	----------	----------	----------	----------	----------	----------	----------
143	----------	----------	----------	----------	----------	----------	----------	----------	----------	----------
147	----------	----------	----------	----------	----------	----------	----------	----------	----------	----------
150	----------	----------	----------	----------	----------	----------	----------	----------	----------	----------
Total and percent	----------	----------	----------	----------	----------	----------	----------	----------	----------	----------
Grand total	37,782	105,273	178,334	214,471	124,528	67,572	7,939	233	736,132	----------
Percent [1]	5.13	14.30	24.22	29.13	16.92	9.18	1.08	0.03	99.99	----------

[1] Hundredths of a percent are used so that trace amounts of spawning may be indicated (see p. 252).

TABLE 5.—*Estimated number (in billions) of jack mackerel eggs in survey area, 1954*

[Cruise numbers in parentheses. No eggs taken during cruise 5412]

	Jan. (5401)	Feb. (5402)	Mar. (5403)	Apr. (5404)	May (5405)	June (5406)	July (5407)	Aug. (5408)	Oct. (5410)	Annual total	Percent of total for all areas
North of Point Conception:											
Lines 40–57	-----	-----	-----	-----	-----	82	-----	-----	-----	82	-----
60–77	-----	-----	-----	0	13, 610	7, 697	9, 685	42	0	31, 034	-----
Total and percent	-----	-----	-----	0	13, 610	7, 779	9, 685	42	0	31, 116	6. 73
Southern California:											
Line 80	0	0	0	43	14, 898	8, 166	4, 937	0	0	28, 044	-----
83	0	0	0	165	25, 822	13, 838	1, 239	31	0	41, 095	-----
85	0	0	0	0	3, 185	9, 797	221	0	0	13, 203	-----
87	0	0	0	17, 090	11, 430	3, 666	52	25	0	32, 263	-----
90	0	0	0	6, 529	3, 894	4, 905	9, 825	1, 596	0	26, 749	-----
93	0	0	0	24, 012	3, 822	1, 010	6, 053	874	16	35, 787	-----
Total and percent	0	0	0	47, 839	63, 051	41, 382	22, 327	2, 526	16	177, 141	38. 31
Northern Baja California:											
Line 97	0	0	7, 846	22, 602	4, 428	11, 690	1, 632	256	0	48, 454	-----
100	0	8, 034	40, 461	21, 729	10, 523	985	7, 289	539	0	89, 560	-----
103	0	878	2, 178	7, 505	11, 424	915	0	0	0	22, 900	-----
105	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
107	0	13, 887	1, 220	4, 029	3, 717	1, 998	0	0	0	24, 851	-----
Total and percent	0	22, 799	51, 705	55, 865	30, 092	15, 588	8, 921	795	0	185, 765	40. 18
Upper central Baja California:											
Line 110	148	208	365	6, 451	6, 622	1, 820	2, 978	0	0	18, 592	-----
113	0	846	4, 137	4, 301	4. 861	538	70	40	0	14, 793	-----
115	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
117	0	464	0	924	585	2, 011	0	33	0	4, 017	-----
120	0	0	208	2, 008	4, 547	4, 671	392	0	0	11, 826	-----
Total and percent	148	1, 518	4, 710	13, 684	16, 615	9, 040	3, 440	73	0	49, 228	10. 65
Lower central Baja California:											
Line 123	0	0	0	124	12, 526	0	0	0	0	12, 650	-----
127	0	0	0	915	207	4	0	0	0	1, 126	-----
130	0	0	0	2, 160	0	0	0	0	0	2, 160	-----
133	0	0	0	2, 984	0	0	0	0	0	2, 984	-----
137	168	0	0	-----	0	0	0	0	0	168	-----
Total and percent	168	0	0	6, 183	12, 733	4	0	0	0	19, 088	4. 13
Southern Baja California:											
Line 140	0	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
143	0	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
147	0	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
150	0	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
Total and percent	0	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
Grand total	316	24, 317	56, 415	123, 571	136, 101	73, 793	44, 373	3, 436	16	462. 338	-----
Percent [1]	0. 07	5. 26	12. 20	26. 73	29. 44	15. 96	9. 60	0. 74	0	100. 00	-----

[1] Hundredths of a percent are used so that trace amounts of spawning may be indicated (see p. 252).

Spawning in 1951 began in February. About 7 percent of the total number of eggs for the season were spawned during this month. Spawning rose to a peak of more than 30 percent of the total in March, and then gradually declined until June, when an increase occurred. Spawning decreased thereafter, being negligible in September. Spawning during February and March was centered about 150 miles offshore in region 2. During the next 2 months spawning was more general and no compact center was observed. Spawning had reached its widest distribution (most of the eggs being taken between lines 60 and 120) in April and May, and the center had moved inshore. During June and July the center was dispersed and offshore.

Spawning in 1952 began in January, when less than 1 percent of the total number of eggs were spawned, and rose to a peak of about 30 percent in May. It then declined to less than 1 percent in September and ceased altogether by October. The center of spawning was about 120 miles farther south during February and March than during the same period of 1951. Once again it was in the intermediate area. During April and May, spawning became heavier in region 3 and there was a strong inshore movement. During the final 2 months the spawners were grouped to

TABLE 6.—*Relative north-south, inshore-offshore distribution of jack mackerel eggs by 2-month intervals for 1951*

[Standard haul totals]

Line	Offshore stations (100-seaward)	Intermediate stations (90–70)	Inshore stations (60-shore)	Total	Percent
February-March:					
60	0	0	0	0	0
70	0	0	0	0	0
80	2,795	7,790	1,658	12,243	33.3
90	1,506	9,013	1,484	12,003	32.6
100	91	955	907	1,953	5.3
110	0	477	10,053	10,530	28.6
120	0	0	74	74	.2
Total	4,392	18,235	14,176	36,803	100.0
Percent	11.9	49.6	38.5	100.0	----------
April-May:					
60	0	14	0	14	.1
70	1,573	27	0	1,600	6.0
80	2,502	629	160	3,291	12.4
90	3,430	1,832	2,976	8,238	31.0
100	589	201	7,312	8,102	30.0
110	647	525	2,505	3,677	13.8
120	847	309	538	1,694	6.4
Total	9,588	3,537	13,491	26,616	99.7
Percent	36.0	13.3	50.7	100.0	----------
June-July:					
60	1,490	222	6	1,718	11.3
70	137	2,613	1,414	4,164	27.5
80	40	1,100	664	1,804	11.9
90	945	284	2,399	3,628	23.9
100	15	1,134	802	1,951	12.9
110	0	765	420	1,185	7.8
120	0	648	56	704	4.6
Total	2,627	6,766	5,761	15,154	99.9
Percent	17.3	44.6	38.0	99.9	----------

TABLE 7.—*Relative north-south, inshore-offshore distribution of jack mackerel eggs by 2-month intervals for 1952*

[Standard haul totals]

Line	Offshore stations (100-seaward)	Intermediate stations (90–70)	Inshore stations (60-shore)	Total	Percent
February-March:					
60	(1)	(1)	(1)	(1)	(1)
70	(1)	(1)	(1)	(1)	(1)
80	11	377	0	388	2.8
90	(1)	6,665	0	6,665	48.5
100	(1)	4,528	2,027	6,555	47.7
110	(1)	4	2	6	<0.1
120	(1)	142	0	142	1.0
Total	11	11,716	2,029	13,756	100.1
Percent	0.1	85.2	14.7	100.0	----------
April-May:					
60	(1)	0	0	0	0
70	(1)	0	0	0	0
80	223	0	0	223	1.0
90	205	3,635	4,805	8,645	37.1
100	82	1,724	6,107	7,913	34.0
110	(1)	5,495	567	6,062	26.0
120	(1)	293	159	452	1.9
Total	510	11,147	11,638	23,295	100.0
Percent	2.2	47.8	50.0	100.0	----------
June-July:					
60	5	535	36	576	3.6
70	429	270	0	699	4.4
80	3,495	2,235	1,098	6,828	42.8
90	74	3,766	950	4,790	30.0
100	161	601	1,208	1,970	12.4
110	(1)	398	665	1,063	6.7
120	(1)	0	13	13	.1
Total	4,164	7,805	3,970	15,939	100.0
Percent	26.1	49.0	24.9	100.0	----------

[1] Region not occupied.

TABLE 8.—*Relative north-south, inshore-offshore distribution of jack mackerel eggs by 2-month intervals for 1953*

[Standard haul totals]

Line	Offshore stations (100-seaward)	Intermediate stations (90–70)	Inshore stations (60-shore)	Total	Percent
February-March:					
60	(1)	(1)	(1)	(1)	(1)
70	(1)	(1)	(1)	(1)	(1)
80	(1)	0	0	0	0
90	(1)	0	0	0	0
100	(1)	1,551	4,445	5,996	51.0
110	(1)	1,138	4,399	5,537	47.1
120	(1)	(1)	228	228	1.9
Total	----------	2,689	9,072	11,761	100.0
Percent	----------	22.9	77.1	100.0	----------
April-May:					
60	0	0	0	0	0
70	(1)	0	8	8	<0.1
80	1,149	2,452	18	3,619	11.7
90	1,725	5,631	298	7,654	24.8
100	(1)	580	805	1,385	4.5
110	(1)	5,437	8,721	14,158	45.8
120	(1)	403	3,679	4,082	13.2
Total	2,874	14,503	13,529	30,906	100.1
Percent	9.3	46.9	43.8	100.0	----------
June-July:					
60	(1)	0	96	96	1.3
70	85	116	61	262	3.4
80	21	703	657	1,381	18.0
90	(1)	423	364	787	10.3
100	151	952	3,456	4,559	59.4
110	(1)	(1)	562	562	7.3
120	(1)	17	10	27	.4
Total	257	2,211	5,206	7,674	100.1
Percent	3.3	28.8	67.8	99.9	----------

[1] Region not occupied.

TABLE 9.—*Relative north-south, inshore-offshore distribution of jack mackerel eggs by 2-month intervals for 1954*

[Standard haul totals]

Line	Offshore stations (100-seaward)	Intermediate stations (90–70)	Inshore stations (60-shore)	Total	Percent
February-March:					
60	(1)	(1)	(1)	(1)	(1)
70	(1)	(1)	(1)	(1)	(1)
80	(1)	0	0	0	0
90	(1)	0	0	0	0
100	(1)	4,167	1,207	5,374	96.5
110	(1)	0	185	185	3.3
120	(1)	12	0	12	0.2
Total	----------	4,179	1,392	5,571	100.0
Percent	----------	75.0	25.0	100.0	----------
April-May:					
60	43	180	0	223	1.7
70	(1)	745	40	785	5.8
80	(1)	2,326	19	2,345	17.4
90	(1)	2,051	616	2,667	19.8
100	987	1,206	1,151	3,344	24.8
110	(1)	351	3,308	3,659	27.1
120	(1)	423	36	459	3.4
Total	1,030	7,282	5,170	13,482	100.0
Percent	7.6	54.0	38.3	99.9	----------
June-July:					
60	50	816	0	866	11.7
70	(1)	48	784	832	11.3
80	347	743	936	2,026	27.5
90	(1)	404	1,931	2,335	31.6
100	(1)	135	367	502	6.8
110	(1)	92	302	394	5.3
120	(1)	270	153	423	5.7
Total	397	2,508	4,473	7,378	99.9
Percent	5.4	34.0	60.6	100.0	----------

[1] Region not occupied.

TABLE 10.—*Comparison of estimates of regional distribution using selected stations on selected lines and all data, 1951–54*

Line	February–March	April–May	June–July	Selected stations		All stations (percent)
				Total	Percent	
1951:						
60	0	14	1,718	1,732	[1] 2.20	12.13
70	0	1,600	4,164	5,764	7.34	
80	12,243	3,291	1,804	17,338	22.07	22.77
90	12,003	8,238	3,628	23,869	30.38	31.53
100	1,953	8,102	1,951	12,006	15.28	16.00
110	10,530	3,677	1,185	15,392	19.59	14.61
120	74	1,694	704	2,472	3.15	2.95
Total				78,573	100.01	99.99
1952:						
60	(2)	0	576	576	1.09	2.64
70	(2)	0	699	699	1.32	
80	388	223	6,828	7,439	14.04	14.78
90	6,665	8,645	4,790	20,100	37.93	40.95
100	6,555	7,913	1,970	16,438	31.02	29.31
110	6	6,062	1,063	7,131	13.46	10.31
120	142	452	13	607	1.15	2.01
Total				52,990	100.01	100.00
1953:						
60	(2)	0	96	96	0.19	1.31
70	(2)	8	262	270	.54	
80	0	3,619	1,381	5,000	9.91	9.76
90	0	7,654	787	8,441	16.77	24.34
100	5,996	1,385	4,559	11,940	23.72	39.07
110	5,537	14,158	562	20,257	40.24	21.43
120	228	4,082	27	4,337	8.62	4.09
Total				50,341	99.99	100.00
1954:						
60	(2)	223	866	1,089	4.12	6.73
70	(2)	785	832	1,617	6.12	
80	0	2,345	2,026	4,371	16.54	24.79
90	0	2,667	2,335	5,002	18.92	24.01
100	5,374	3,344	502	9,220	34.88	29.70
110	185	3,659	394	4,238	16.03	8.09
120	12	459	423	894	3.38	6.69
Total				26,431	99.99	100.01

[1] Hundredths of a percent are used so trace amounts of spawning may be indicated (see p. 252).

[2] Region not occupied.

the north in region 2 and were farther offshore in the intermediate area.

Spawning in 1953 began in February and rose to a peak of nearly 30 percent of the total in May, and then declined. Only small numbers of eggs were taken in October. Early spawning was centered in region 3, with a fair amount in region 2. The center of spawning was about 240 miles farther south than the early spawning of 1951, and most of the spawning was inshore. From this center, spawning moved both north and south and somewhat offshore to the intermediate area. During the final 2 months, the center of spawning was again in region 3 and inshore.

The monthly distribution of spawning for 1954 is very similar to that for 1953. Spawning extended from January to October and reached a peak of nearly 30 percent of the total in May. Early spawning was centered in region 3 about 150 miles offshore (intermediate area) and no eggs were taken off California. In the next 2 months the heavier concentrations extended north to region 2 and south to the northern edge of region 4, with some inshore movement. During the final 2 months the center shifted northward to region 2 and inshore. The distribution and relative abundance of jack mackerel eggs for 1951–54 are illustrated in Farris (1958: figs. 3–6).

The remarkable similarity of monthly distribution of spawning in 1952 through 1954 (peak month, May) is illustrated in figure 4. The year 1951 appears to have been an anomalous year with an early peak of spawning in March. The proportion of spawning that occurred during the peak month of each year, including 1951, was approximately three-tenths of the total for the year. Furthermore, over seven-tenths of the spawning for any year occurred during the first 5 months.

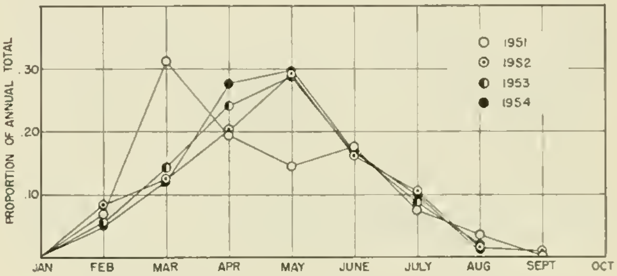

FIGURE 4.—Proportion of annual spawning of jack mackerel, by months, 1951–54.

Of the 4 years studied, 1951 had the highest proportion of the annual total number of eggs in region 1. High proportions of the annual total eggs were found in regions 3 and 4 during 1953, with a small proportion being taken in regions 1 and 2.

BOUNDARIES OF THE SPAWNING AREA

The northern and western boundaries of jack mackerel spawning during August and September were established by expedition *Norpac*, an extensive study of the north Pacific in 1955 conducted by the California Cooperative Oceanic Fisheries Investigations and other agencies (Ahlstrom, 1956: p. 39; Ahlstrom and Kramer, 1957: p. 55). These boundaries may be less certain than the others because the study of the area was more limited in time. The eastern and southern boundaries were established from data collected on regular survey cruises of the California Cooperative Oceanic Fisheries Investigations (Farris, 1958). Spawning areas are approximately bounded by the 26th parallel on the south, the 45th parallel on the north, the coast of North America on the east, and the 150th meridian on the west.

SOURCES OF ERROR AND BIAS IN SAMPLING EGGS

These data and subsequent interpretations are subject to errors inherent in the collection procedures. The types of error investigated and evaluated were (1) completeness of retention of eggs by the nets; (2) completeness of sampling of the vertical range; (3) sampling error owing to a variable distribution of eggs in space and time; and (4) incomplete sampling of the horizontal range of jack mackerel spawning.

RETENTION OF EGGS BY THE NETS

The eggs are fully retained by the net once they are in it, because the plankton nets have a stretched mesh of 0.5–0.7 mm. (Ahlstrom, 1953), and the spherical eggs range in diameter from 0.9–1.1 mm (Ahlstrom and Ball, 1954). It would appear, therefore, that no eggs are lost through the mesh of the sampling net.

SAMPLING OF THE VERTICAL RANGE

Investigation of the vertical distribution of jack mackerel eggs (Ahlstrom, 1959: table 7) with a horizontally towed closing net reveals that most of the eggs occur in the upper 40 meters of water. Jack mackerel eggs have rarely been taken below 100 meters, and never below 140 meters. The bulk of the eggs have occurred above the thermocline. Since plankton hauls are routinely made from a depth of 140 meters, which has always included the thermocline depth, it seems likely that the vertical distribution of jack mackerel eggs is completely sampled.

VARIABLE DISTRIBUTION OF EGGS

The distribution of jack mackerel eggs is variable with respect to both time and space. An illustrative example is given in figure 5. The standard numbers of jack mackerel eggs for line 97 have been plotted by station for 4 months. The average number of eggs per station by month is given below.

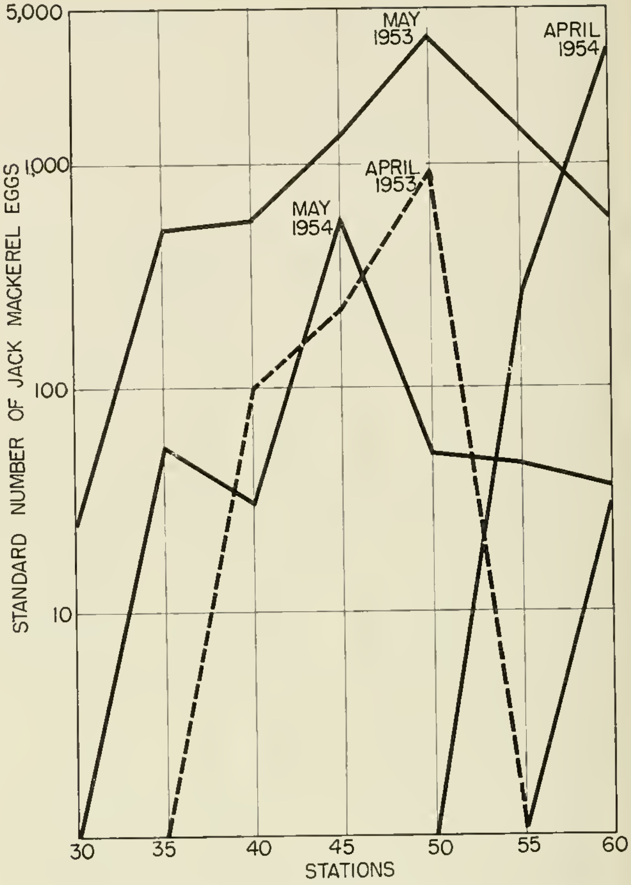

FIGURE 5.—Standard numbers of jack mackerel eggs found on line 97 during 4 months.

Year:	*April*	*May*
1953	181	1, 116
1954	762	143

The average station on line 97 in May 1953 contained six times as many eggs as the average station in the preceding month. Assuming that this change was rectilinear in time, the estimate would be altered considerably, depending on which day of the month the sample was taken.

Spatial variability is indicated by the data for April 1954, in which a change of 1 order of magnitude occurs within 20 miles. There is at least one such combination of adjacent stations having as great a change in the distribution of jack mackerel eggs for each cruise illustrated. The grid of stations occupied is too coarse except for fairly rough estimates of egg abundance. Although more frequent sampling of more closely spaced stations is highly desirable, such sampling cannot be effected, since it would raise the current cost of sampling prohibitively.

The monthly sampling of the California Cooperative Oceanic Fisheries Investigations grid of stations has all but precluded the simple assessment of the error associated with these estimates of abundance. Although the construction of the proper statistical model was not within the scope of this investigation, I was able to make an estimate of the error arising from the practice of linear interpolation of egg numbers in time and space. This calculation was possible because in 1953 and 1954 stations which were only 20 miles apart were occupied, and the samples contained jack mackerel eggs. In 1952, a few stations containing jack mackerel eggs were occupied in late March.

The errors arising from stratification in space (i.e., spacing sampling stations 40 miles apart) and time (i.e., spacing sampling cruises 1 month apart) were considered. Standard numbers of eggs for stations 20 miles apart—obtained by linear interpolation of values obtained from stations 40 miles apart—were compared with values actually observed. In like manner, standard numbers of eggs for stations sampled at intervals of one-half month—obtained by linear interpolation of observed values from stations sampled at monthly intervals—were compared with the values actually observed. The differences should be zero if no error arises from linear interpolation through space and time. Since the average difference cannot be expected actually to equal zero, owing to sampling variability, the 95-percent confidence limits for both estimates were computed. These limits should include zero.

The error arising from spacing the sampling stations 40 miles apart was estimated using data from selected stations on selected lines. (Stations having no eggs were not used.) These stations were placed 20 miles apart. An estimated value was given for every other station by a process of linear interpolation of values between the remaining stations which were 40 miles apart. These interpolated values were then compared with the actual number of eggs found at the stations and the difference (Δ_i) calculated. (Δ_i=observed standard number of jack mackerel eggs minus estimated number of jack mackerel eggs.) The deltas were averaged to give $\bar{\Delta}$, the average difference between the observed standard number of jack mackerel eggs and the number calculated by linear interpolation.

The frequency distribution of Δ_i was plotted and appeared to be normally distributed (fig. 6).

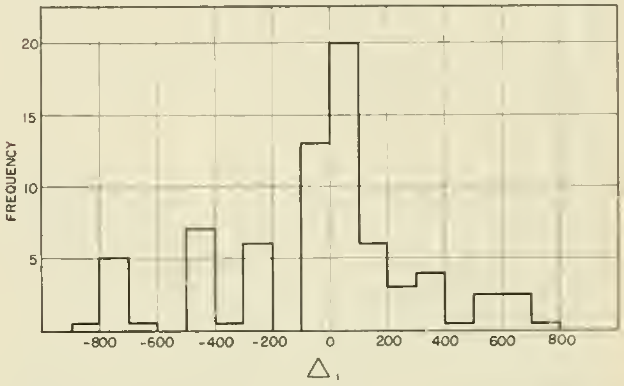

FIGURE 6.—Frequency distribution of Δ_i (the difference between observed and estimated numbers of jack mackerel eggs).

Therefore Δ_i was considered to be a normally distributed random variable with mean $\bar{\Delta}$ and variance s^2.

Statistic	Value	Description
$\bar{\Delta}$	7.8	Average difference.
$s^2\Delta_i$	518,956	Variance of the individual differences.
$s\Delta_i$	720	Standard deviation of the individual differences.
$s_{\bar{\Delta}}$	74.2	Standard deviation of the mean.
n	94	Number of differences observed.

$$-137.2 \leqq \bar{\Delta} \leqq 152.8$$

The average difference is close to zero. The wide confidence limits indicate the high variability associated with any one observation.

The Δ_i were compared with the size of each ith haul to determine whether the differences were related to population size (fig. 7). No relation was evident and it was concluded that the Δ_i were not related to population size.

The error arising from stratification in time was estimated by considering the standard numbers of jack mackerel eggs taken at selected stations during cruises spaced about 2 weeks apart (March, late March, and April, 1952). By linear interpolation of the number of eggs taken at a station between the March and April occupancies, an estimate of the number of eggs that should occur at the station during the late March occupancy was obtained. This estimated number was then

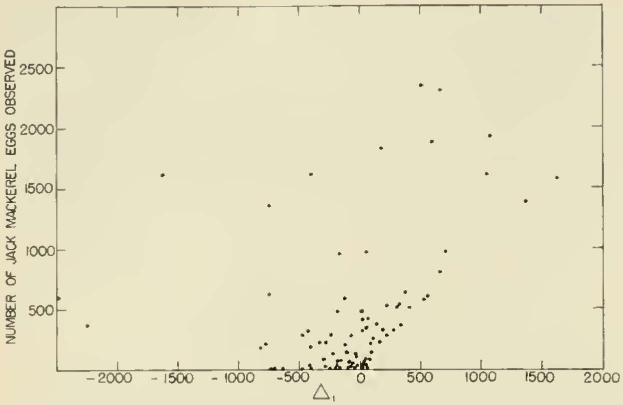

Figure 7.—Relation of Δ_i (the difference between observed and estimated numbers of jack mackerel eggs) and the number of eggs observed at the ith station.

compared with the number actually observed and the difference (Δ_i) noted. (Δ_i=the standard number of jack mackerel eggs estimated by linear interpolation minus the number actually observed.) The differences were averaged to give a mean difference ($\bar{\Delta}$) between the estimated number of eggs and the actual number of eggs. The average difference ($\bar{\Delta}$) was minus 11, with a variance of 3370. The 95-percent confidence limits on $\bar{\Delta}$ are minus 47 to plus 25.

Although the individual errors arising from the practice of linear interpolation of jack mackerel eggs in time and space were high and variable, the average error tended toward zero. I concluded that for a large number of samples (i.e., interpolations) the error arising from linear interpolation of the number of eggs in time and space was negligible.

A further indication of irregularities in the spatial and/or temporal distribution would be the nonconcurrence of eggs and larvae in the sampling areas. In table 11 the occurrences of eggs and larvae, by regions, are compared. In region 1,

Table 11.—*Occurrences of jack mackerel eggs and larvae, by month and region, 1952–54*

Date	Region 1[1]			Region 2			Region 3			Region 4			Region 5			Region 6		
	Stations occupied	Stations with eggs	Stations with larvae	Stations occupied	Stations with eggs	Stations with larvae	Stations occupied	Stations with eggs	Stations with larvae	Stations occupied	Stations with eggs	Stations with larvae	Stations occupied	Stations with eggs	Stations with larvae	Stations occupied	Stations with eggs	Stations with larvae
1952:																		
January	------	------	------	28	0	0	19	3	1	22	0	0	25	0	0	------	------	------
February	------	------	------	27	5	3	20	7	0	30	0	0	18	0	0	14	0	0
March	------	------	------	25	4	6	20	8	12	25	7	11	21	1	3	------	------	------
April	18	0	0	37	14	12	31	24	26	36	17	13	33	5	10	------	------	------
May	23	0	0	50	31	28	43	35	37	40	30	25	31	5	7	------	------	------
June	34	4	3	58	36	42	58	34	42	42	21	18	30	3	3	------	------	------
July	46	14	4	38	31	22	32	27	25	36	9	11	27	0	2	------	------	------
August	15	2	1	22	10	8	17	3	9	30	1	0	15	0	0	------	------	------
September	21	0	0	22	6	8	17	5	3	19	0	0	15	0	0	------	------	------
October	18	0	0	21	0	1	15	0	2	19	0	0	15	0	0	------	------	------
November	18	0	0	22	0	0	16	0	0	21	0	0	14	0	0	------	------	------
December	------	------	------	------	------	------	------	------	------	------	------	------	------	------	------	------	------	------
Total	193	20	8	350	137	130	288	146	157	320	85	78	244	14	25	14	0	0
1953:																		
January	------	------	------	34	0	0	20	0	0	16	0	0	13	0	0	13	0	0
February	------	------	------	35	0	1	17	2	4	24	8	5	19	0	0	------	------	------
March	------	------	------	36	0	3	17	9	13	29	11	12	31	0	1	------	------	------
April	20	1	0	61	9	8	41	30	21	38	31	18	35	0	0	------	------	------
May	30	0	0	63	41	23	38	35	22	37	28	21	35	8	10	------	------	------
June	26	18	2	56	31	20	43	33	34	40	19	23	31	11	9	------	------	------
July	24	9	2	38	21	15	20	14	8	21	8	5	19	0	0	------	------	------
August	19	6	1	38	11	5	20	8	3	21	3	2	20	0	0	------	------	------
September	------	------	------	18	0	1	------	------	------	24	0	0	------	------	------	------	------	------
October	------	------	------	18	2	3	16	2	6	21	0	4	14	0	1	------	------	------
November	------	------	------	19	0	0	------	------	------	------	------	------	------	------	------	------	------	------
December	------	------	------	28	0	0	17	0	0	21	0	0	16	0	0	------	------	------
Total	119	34	5	444	115	79	249	133	111	292	108	90	233	19	21	13	0	0
1954:																		
January	2	0	0	42	0	0	22	0	0	27	1	0	23	1	2	18	0	0
February	2	0	0	37	0	0	24	11	3	31	5	4	22	0	1	------	------	------
March	2	0	0	35	0	0	32	15	19	48	8	19	36	0	0	------	------	------
April	18	0	0	51	16	13	39	29	26	52	24	19	38	8	15	------	------	------
May	19	8	2	54	33	23	42	34	34	52	25	29	38	9	8	------	------	------
June	36	13	9	48	31	20	39	25	34	51	17	22	35	1	6	------	------	------
July	19	8	6	37	13	11	20	9	9	22	6	3	20	0	1	------	------	------
August	22	1	2	39	10	13	19	6	8	22	2	0	20	0	0	------	------	------
September	------	------	------	------	------	------	------	------	------	------	------	------	------	------	------	------	------	------
October	2	0	0	38	2	1	22	0	0	23	0	0	20	0	1	------	------	------
November	------	------	------	------	------	------	------	------	------	------	------	------	------	------	------	------	------	------
December	------	------	------	36	0	0	16	0	0	26	0	0	19	0	0	18	0	0
Total	122	30	19	417	105	81	275	129	133	354	88	96	271	19	34	36	0	0

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[1] See page 253.

there are more occurrences of eggs than of larvae, while in region 5, the converse is true. This may indicate southern transport of the larvae by the California Current.

The high proportion of stations occupied in region 2 at which eggs or larvae were taken is a further indication (see also tables 3, 4, and 5) that this is the region of maximum spawning activity.

A comparison of total occurrences of eggs with total occurrences of larvae is interpreted as indicative of a distribution more regular than that encountered for other pelagic eggs and larvae (e.g., sardines).

SAMPLING OF THE HORIZONTAL RANGE OF SPAWNING

To determine the proportion of the total annual spawning which might be missed by failure to extend the sampling far enough seaward, the proportion of eggs taken beyond stations 90 (the usual seaward extent of sampling) was computed (see column 100—seaward in tables 6, 7, 8, and 9). This areal proportion was multiplied by the proportion of annual spawning that occurred during the appropriate 2-month interval (tables 2, 3, 4, and 5) to give a bimonthly estimate of the proportion of annual spawning which might be missed by failure to extend the sampling sufficiently seaward (table 12). It would appear that at least 21 percent of the annual spawning has occurred seaward of stations 90, and that a portion of the eggs has been missed in those years when monthly sampling was not extended beyond that point.

Table 12.—*Proportion of jack mackerel spawning occurring seaward of station 90, by 2-month intervals, 1951–54*

Month	1951	1952	1953	1954
February-March	0.05	(1)	(1)	(1)
April-May	.12	0.01	0.05	0.04
June-July	.04	.07	.01	.01
Annual total	.21	.08	.06	.05

[1] Region not occupied.

Data from the previously mentioned *Norpac* indicate that the proportion of eggs spawned in northern waters (north of line 40) may be between 1 and 2 percent of the annual total. This proportion is minimal, since spawning occurs in periods other than that covered by *Norpac*. This estimate was determined by estimating the total spawning in the region for the period August–early September (8,655 billion eggs) and comparing that figure with the estimated number of eggs spawned in 1954 (464,452 billion) and 1951 (874,322 billion). It is therefore inferred that an appreciable amount of annual spawning may occur west of stations 90 but a lesser amount takes place north of line 40.

EFFECTS OF TEMPERATURE ON SPAWNING

Temperature may have at least two effects on the jack mackerel. It influences the rate at which the eggs develop (see p. 250), and it may well govern when and where the adults spawn.

To determine the effect of temperature on the spawning jack mackerel, temperatures at 10-meter depths were tabulated by 0.5° C. intervals for all stations where jack mackerel eggs were taken in 1951 through 1954 (table 13). The temperature at this depth is generally representative of the strata in which jack mackerel eggs are most abundant. These data were examined also for seasonal effect by dividing the year into an early (January–May) and a late (June–December) period. The effect of temperature on the size of haul was also examined by dividing the samples into two categories: hauls containing 1–100 eggs and hauls containing 101 eggs and more.

A seasonal trend toward higher spawning temperatures in the late summer with a greater temperature range was indicated (table 14 and figure 8). The data were then tabulated by

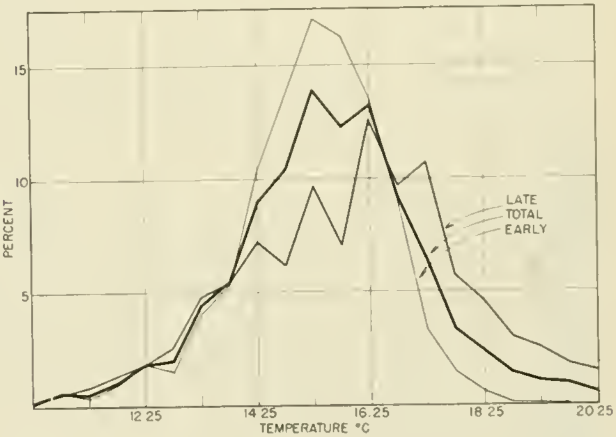


Figure 8.—Percentage of early (January-May) stations, of late (June–December) stations, and of the total stations having jack mackerel eggs, shown by 0.5° C. temperature intervals measured at 10-meter depth.

TABLE 13.—*Temperature distribution at 10 meters of stations having jack mackerel eggs, by season and size of sample, 1951–54*

[In 0.5° C. intervals]

Temperature	1951			1952			1953			1954			Total			Percent of total
	Early	Late	Total	Early	Late	Total	Early	Late	Total	Early	Late	Total	Early	Late	Total	
1–100 eggs:																
10.00–10.49	0	0	0	0	1	1	1	0	1	0	0	0	1	1	2	0.2
10.50–10.99	0	2	2	0	0	0	4	1	5	1	0	1	5	3	8	1.1
11.00–11.49	1	2	3	0	1	1	0	1	1	1	1	2	2	5	7	1.0
11.50–11.99	2	1	3	0	1	1	1	1	2	3	3	6	6	6	12	1.7
12.00–12.49	3	4	7	1	1	2	4	4	8	0	1	1	8	10	18	2.5
12.50–12.99	3	2	5	1	5	6	2	4	6	1	0	1	7	11	18	2.5
13.00–13.49	9	5	14	3	4	7	1	5	6	2	4	6	15	18	33	4.6
13.50–13.99	10	3	13	7	2	9	6	7	13	1	3	4	24	15	39	5.5
14.00–14.49	6	6	12	4	3	7	7	5	12	10	6	16	27	20	47	6.6
14.50–14.99	4	3	7	4	6	10	5	5	10	11	3	14	24	17	41	5.7
15.00–15.49	10	11	21	13	7	20	10	10	20	17	6	23	50	34	84	11.7
15.50–15.99	15	11	26	6	5	11	4	6	10	13	1	14	38	23	61	8.5
16.00–16.49	17	17	34	11	15	26	8	10	18	17	9	26	53	51	104	14.5
16.50–16.99	14	8	22	8	14	22	4	4	8	13	12	25	39	38	77	10.7
17.00–17.49	9	12	21	2	20	22	1	6	7	8	6	14	20	44	64	9.0
17.50–17.99	6	6	12	1	3	4	1	5	6	0	6	6	8	20	28	3.9
18.00–18.49	5	3	8	0	5	5	0	5	5	0	7	7	5	20	25	3.5
18.50–18.99	1	6	7	0	1	1	0	3	3	0	6	6	1	16	17	2.4
19.00–19.49	0	2	2	0	1	1	0	5	5	0	2	2	0	10	10	1.4
19.50–19.99	0	1	1	0	0	0	0	3	3	1	6	7	1	10	11	1.5
20.00–20.49	0	0	0	0	1	1	0	2	2	0	4	4	0	7	7	1.0
20.50–20.99	0	1	1	0	0	0	0	1	1	0	0	0	0	2	2	.2
Total	115	106	221	61	96	157	59	93	152	99	86	185	334	381	715	99.7
101+ eggs:																
10.00–10.49	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
10.50–10.99	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
11.00–11.49	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
11.50–11.99	0	1	1	0	0	0	1	1	2	0	0	0	1	2	3	.4
12.00–12.49	2	1	3	1	0	1	3	0	3	0	0	0	6	1	7	1.0
12.50–12.99	1	2	3	0	1	1	2	0	2	2	2	4	5	5	10	1.5
13.00–13.49	4	2	6	5	6	10	2	2	4	6	2	8	17	11	28	4.1
13.50–13.99	7	8	15	2	2	4	6	3	9	3	5	8	18	18	36	5.3
14.00–14.49	19	11	30	8	1	9	13	6	19	14	6	20	54	24	78	11.4
14.50–14.99	14	3	17	25	10	35	21	6	27	24	2	26	84	21	105	15.4
15.00–15.49	29	3	32	8	7	15	25	11	36	23	4	27	85	25	110	16.2
15.50–15.99	23	4	27	22	7	29	24	8	32	22	1	23	91	20	111	16.3
16.00–16.49	20	9	29	14	6	20	7	8	15	13	3	16	54	26	80	11.7
16.50–16.99	6	6	12	7	9	16	5	4	9	13	2	15	31	21	52	7.6
17.00–17.49	1	4	5	2	6.	8	2	8	10	1	3	4	6	21	27	4.0
17.50–17.99	1	3	4	1	7	8	1	5	6	0	0	0	3	15	18	2.6
18.00–18.49	0	4	4	0	1	1	0	3	3	0	0	0	0	8	8	1.2
18.50–18.99	0	0	0	0	0	0	0	2	2	0	0	0	0	2	2	.3
19.00–19.49	0	0	0	0	1	1	0	4	4	0	0	0	0	5	5	.7
19.50–19.99	0	0	0	0	0	0	0	0	0	0	1	1	0	1	1	.1
20.00–20.49	0	0	0	0	1	1	0	0	0	0	1	1	0	2	2	.3
20.50–20.99	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Total	127	61	188	95	64	159	112	71	183	121	32	153	455	228	683	100.1

TABLE 14.—*Summary: Distribution of temperatures at 10 meters of stations having jack mackerel eggs, by season and size of sample, 1951–54*

[In 0.5°C. intervals]

Temperature	Early season				Late season				Season total			
	1–100 eggs	101+ eggs	Total	Percent of total	1–100 eggs	101+ eggs	Total	Percent of total	1–100 eggs	101+ eggs	Total	Percent of total
10.00–10.49	1	0	1	0.1	1	0	1	0.2	2	0	2	0.1
10.50–10.99	5	0	5	.6	3	0	3	.5	8	0	8	.6
11.00–11.49	2	0	2	.3	5	0	5	.8	7	0	7	.5
11.50–11.99	6	1	7	.9	6	2	8	1.3	12	3	15	1.1
12.00–12.49	8	6	14	1.8	10	1	11	1.8	18	7	25	1.8
12.50–12.99	7	5	12	1.5	11	6	16	2.6	18	10	28	2.0
13.00–13.49	15	17	32	4.1	18	11	29	4.8	33	28	61	4.4
13.50–13.99	24	18	42	5.3	15	18	33	5.4	39	36	75	5.4
14.00–14.49	27	54	81	10.3	20	24	44	7.2	47	78	125	8.9
14.50–14.99	24	84	108	13.7	17	21	38	6.2	41	105	146	10.4
15.00–15.49	50	85	135	17.1	34	25	59	9.7	84	110	194	13.9
15.50–15.99	38	91	129	16.3	23	20	43	7.1	61	111	172	12.3
16.00–16.49	53	54	107	13.6	51	26	77	12.6	104	80	184	13.2
16.50–16.99	39	31	70	8.9	38	21	59	9.7	77	52	129	9.2
17.00–17.49	20	6	26	3.3	44	21	65	10.7	64	27	91	6.5
17.50–17.99	8	3	11	1.4	20	15	35	5.7	28	18	46	3.3
18.00–18.49	5	0	5	.6	20	8	28	4.6	25	8	33	2.4
18.50–18.99	1	0	1	.1	16	2	18	3.0	17	2	19	1.4
19.00–19.49	0	0	0	0	10	5	15	2.5	10	5	15	1.1
19.50–19.99	1	0	1	.1	10	1	11	1.8	11	1	12	.9
20.00–20.49	0	0	0	0	7	2	9	1.5	7	2	9	.6
20.50–20.99	0	0	0	0	2	0	2	.3	2	0	2	.1
Total	334	455	789	100.0	381	228	609	100.0	715	683	1,398	100.1

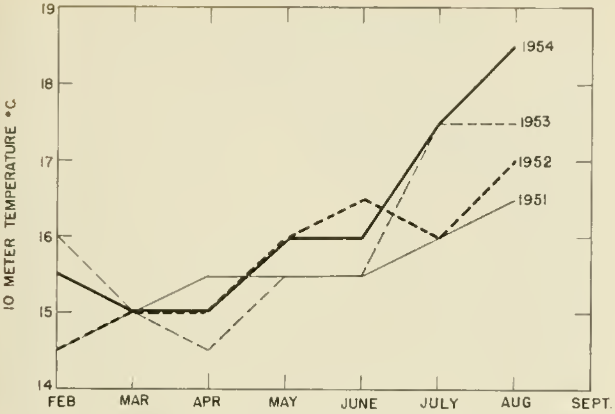


FIGURE 9.—Monthly median temperatures at 10 meters, at which jack mackerel eggs were spawned.

monthly intervals and the median temperatures at 10 meters computed for each month. The monthly median temperatures are shown in figure 9 and indicate that spawning generally occurs at lower temperatures in spring than in late summer. The within-year median temperature shift is greater than the between-year temperature variation (see below).

The data from table 13 are summarized in tables 15 and 16. A difference in optimum spawning temperature between small hauls (1–100 eggs) and large hauls (101 eggs and more) is noted (fig. 10). The reason for the difference is that a large proportion of the large hauls were taken during the peak of the season (April and May), and have therefore a more restricted temperature distribution.

TABLE 15.—*Summary: Distribution of temperatures at 10 meters of stations having jack mackerel eggs, by size of sample, 1951–54*

[In 0.5° C. intervals]

Temperature	1–100 eggs	101+ eggs	Total samples	Percent of total
10.00–10.49	2	0	2	0.1
10.50–10.99	8	0	8	.6
11.00–11.49	7	0	7	.5
11.50–11.99	12	3	15	1.1
12.00–12.49	18	7	25	1.8
12.50–12.99	18	10	28	2.0
13.00–13.49	33	28	61	4.4
13.50–13.99	39	36	75	5.4
14.00–14.49	47	78	125	9.0
14.50–14.99	41	105	146	10.4
15.00–15.49	84	110	194	13.9
15.50–15.99	61	111	172	12.3
16.00–16.49	104	80	184	13.2
16.50–16.99	77	52	129	9.2
17.00–17.49	64	27	91	6.5
17.50–17.99	28	18	46	3.3
18.00–18.49	25	8	33	2.4
18.50–18.99	17	2	19	1.4
19.00–19.49	10	5	15	1.1
19.50–19.99	11	1	12	.9
20.00–20.49	7	2	9	.6
20.50–20.99	2	0	2	.1
Total	715	683	1,398	100.2

TABLE 16.—*Average temperatures at 10 meters during jack mackerel spawning, by season and size of sample, 1951–54*

Sample size and spawning season	Mean	Median	Mode
1951:			
1–100 eggs:			
Early	15.5	15.5	16.0
Late	15.8	16.0	16.0
Annual average	15.7	15.5	16.0
101+ eggs:			
Early	15.2	15.0	15.0
Late	15.4	15.0	14.0
Annual average	15.3	15.0	15.0
1952:			
1–100 eggs:			
Early	15.3	15.0	15.0
Late	16.0	16.0	17.0
Annual average	15.7	16.0	16.0
101+ eggs:			
Early	15.3	15.0	14.5
Late	15.9	15.5	14.5
Annual average	15.6	15.5	14.5
1953:			
1–100 eggs:			
Early	14.5	14.5	15.0
Late	15.9	15.5	16.0
Annual average	15.3	15.0	15.0
101+ eggs:			
Early	15.1	15.0	15.0
Late	16.1	15.5	15.0
Annual average	15.5	15.0	15.0
1954:			
1–100 eggs:			
Early	15.5	16.0	16.0
Late	16.6	16.5	16.5
Annual average	16.0	16.0	16.0
101+ eggs:			
Early	15.2	15.0	14.5
Late	15.2	15.0	14.0
Annual average	15.2	15.0	15.0
All years:			
1–100 eggs:			
Early	15.2	15.5	16.0
Late	16.0	16.0	16.0
Annual average	15.7	15.5	16.0
101+ eggs:			
Early	15.2	15.0	15.5
Late	15.7	15.0	15.0
Annual average	15.4	15.5	15.5

The early, late, and annual distributions of temperature at a depth of 10 meters, by 0.5° C. increments, for all stations occupied in 1951–54 are given in table 17. These differ from the distribution of temperatures at which jack mackerel were taken in two ways: their temperature range is greater, and they show less tendency to cluster about a central value.

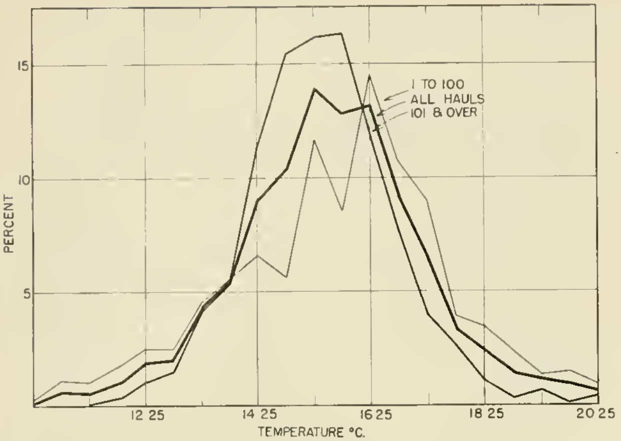


Figure 10.—Percentage of stations having jack mackerel eggs, grouped by 0.5° C. temperature intervals measured at 10-meter depth for stations with hauls of 1–100 eggs, with hauls of 101 eggs and more, and for all stations where eggs were taken.

All jack mackerel data were then combined for each year and the mean, median, and modal temperatures at 10 meters were computed (table 18). The mean and median temperatures for the 4 years are remarkably constant (15.5° C.) with about 60 percent of the annual spawning occurring within 1° of the median and mean. Less than 40 percent of all the stations occupied during the spawning season (February through July) had temperatures within 1° of 15.5° C. (table 19). The constancy of annual temperature medians and means would indicate a sharp temperature optimum for spawning were it not for the within-year temperature shift. The within-year temperature shift suggests that a physiological temperature optimum for jack mackerel is a function of many environmental factors, such as condition of the fish and availability of food, to mention two possibilities. Furthermore, if temperature is the controlling factor, spawning should occur more or less uniformly throughout the area having the optimum temperature. A temperature of 15.5° C. is usually present in the waters off California or Baja California, but spawning occurs only during spring and summer. This may indicate that the length of day has some regulatory effect on spawning.

Table 17.—*Summary: Distribution of temperatures at 10 meters, by season, at stations occupied, 1951–54*

[In 0.5° C. intervals]

Temperature	1951			1952			1953			1954			Total for all years	Percent of total
	Early	Late	Total	Early	Late	Total	Early	Late	Total	Early	Late	Total		
8.00–8.49	0	0	0	0	0	0	0	0	0	0	1	1	1	0.02
8.50–8.99	0	2	2	0	0	0	0	0	0	0	0	0	2	.04
9.00–9.49	0	0	0	1	0	1	3	1	4	0	1	1	6	.11
9.50–9.99	1	3	4	3	1	4	8	3	11	2	1	3	22	.40
10.00–10.49	2	8	10	5	11	16	7	4	11	2	6	8	45	.83
10.50–10.99	6	4	10	7	9	16	10	5	15	2	3	5	46	.85
11.00–11.49	12	10	22	6	20	26	18	9	27	7	6	13	88	1.62
11.50–11.99	13	7	20	5	14	19	37	5	42	13	6	19	100	1.84
12.00–12.49	18	9	27	19	21	40	52	12	64	19	11	30	161	2.96
12.50–12.99	13	7	20	31	26	57	59	21	80	35	14	49	206	3.79
13.00–13.49	36	15	51	35	31	66	59	21	80	46	16	62	259	4.76
13.50–13.99	50	19	69	49	20	69	78	37	115	64	21	85	338	6.22
14.00–14.49	50	33	83	59	27	86	72	42	114	93	30	123	406	7.48
14.50–14.99	42	30	72	70	31	101	75	36	111	94	29	123	407	7.49
15.00–15.49	71	49	120	62	46	108	60	54	114	94	43	137	479	8.71
15.50–15.99	66	51	117	61	35	96	65	41	106	96	39	135	454	8.35
16.00–16.49	63	52	115	53	50	103	35	50	85	61	65	126	429	7.89
16.50–16.99	53	45	98	43	50	93	29	38	67	43	54	97	355	6.53
17.00–17.49	47	43	90	30	57	87	21	43	64	31	56	87	328	6.03
17.50–17.99	36	49	85	24	39	63	21	39	60	15	39	54	262	4.82
18.00–18.49	21	45	66	7	41	48	6	33	39	18	55	73	226	4.16
18.50–18.99	9	40	49	8	33	41	8	28	36	11	36	47	173	3.16
19.00–19.49	3	30	33	4	30	34	7	29	36	11	18	29	132	2.41
19.50–19.99	6	29	35	12	18	30	2	16	18	5	37	42	125	2.30
20.00–20.49	0	18	18	5	13	18	1	12	13	0	31	31	80	1.47
20.50–20.99	1	21	22	5	17	22	2	9	11	1	11	12	67	1.23
21.00–21.49	2	10	12	3	15	18	4	8	12	1	10	11	53	.98
21.50–21.99	1	8	9	2	11	13	5	4	9	1	5	6	37	.68
22.00–22.49	2	8	10	1	6	7	0	5	5	0	5	5	27	.50
22.50–22.99	0	8	8	0	3	3	0	4	4	0	6	6	21	.39
23.00–23.49	0	6	6	1	6	7	0	0	0	0	3	3	16	.29
23.50–23.99	0	9	9	0	4	4	0	3	3	0	8	8	24	.44
24.00–24.49	0	8	8	0	6	6	0	1	1	0	0	0	15	.27
24.50–24.99	0	8	8	0	1	1	0	0	0	0	0	0	9	.16
25.00–25.49	0	2	2	0	0	0	0	1	1	0	0	0	3	.06
25.50–25.99	0	8	8	0	0	0	0	2	2	0	2	2	12	.22
26.00–26.49	0	8	8	0	0	0	0	1	1	0	1	1	10	.18
26.50 and over	0	15	15	0	0	0	0	2	2	0	0	0	17	.31
Total	624	717	1,341	611	692	1,303	744	619	1,363	765	669	1,434	5,441	99.95

Table 18.—*Annual mean, median, and modal temperatures at which spawning occurred, 1951–54*

[At 10 meters; in °C.]

Year	Median and mean temperature	Percent spawning within 1° of median	Mode
1951	15.5	58	16.3
1952	15.5	65	16.3
1953	15.5	60	15.3
1954	15.5	63	15.3

Table 19.—*Summary: Distribution of temperatures at 10 meters, at all stations occupied, February through July, 1951–54*

[In 0.5°C. intervals]

Temperature	1951		1952		1953		1954	
	Total	Percent	Total	Percent	Total	Percent	Total	Percent
8.00–8.49	0	0	0	0	0	0	1	0.10
8.50–8.99	0	0	0	0	0	0	0	0
9.00–9.49	0	0	1	0.12	4	0.44	1	.10
9.50–9.99	2	0.27	4	.49	10	1.10	3	.30
10.00–10.49	7	.95	13	1.60	10	1.10	8	.81
10.50–10.99	7	.95	11	1.35	15	1.65	5	.51
11.00–11.49	10	1.36	20	2.46	25	2.74	12	1.21
11.50–11.99	16	2.18	16	1.97	40	4.39	19	1.92
12.00–12.49	20	2.72	34	4.18	61	6.70	25	2.53
12.50–12.99	16	2.18	37	4.55	63	6.92	38	3.84
13.00–13.49	35	4.76	50	6.15	61	6.70	51	5.16
13.50–13.99	50	6.80	50	6.15	86	9.34	63	6.38
14.00–14.49	61	8.30	60	7.37	79	8.66	92	9.30
14.50–14.99	46	6.26	87	10.70	76	8.34	92	9.30
15.00–15.49	77	10.49	75	9.23	87	9.55	102	10.31
15.50–15.99	76	10.35	67	8.24	77	8.35	105	10.62
16.00–16.49	80	10.90	76	9.35	49	5.38	97	9.81
16.50–16.99	61	8.30	69	8.49	41	4.50	79	7.99
17.00–17.49	48	6.53	53	6.52	43	4.72	62	6.27
17.50–17.99	35	4.76	32	3.94	29	3.18	32	3.24
18.00–18.49	36	4.90	18	2.22	15	1.65	35	3.54
18.50–18.99	17	2.31	12	1.48	17	1.87	25	2.53
19.00–19.49	5	.68	6	.74	11	1.21	16	1.62
19.50–19.99	10	1.36	8	.98	3	.33	15	1.52
20.00–20.49	5	.68	3	.37	4	.44	7	.71
20.50–20.99	5	.68	3	.37	3	.33	2	.20
21.00–21.49	3	.41	2	.25	1	.11	0	0
21.50–21.99	1	.14	4	.49	1	.11	1	.10
22.00–22.49	4	.54	1	.12	0	0	0	0
22.50–22.99	1	.14	0	0	0	0	0	0
23.00–23.49	0	0	1	.12	0	0	1	.10
23.50–23.99	0	0	0	0	0	0	0	0
24.00–24.49	1	.14	0	0	0	0	0	0
24.50–24.99	0	0	0	0	0	0	0	0
25.00–25.49	0	0	0	0	0	0	0	0

Turner (1948: p. 351) says, "The reproductive rhythms of the female, as in the male, are influenced by numerous factors in the external environment as well as by physiologic factors conditioning the internal environment." Since little is known about the internal factors governing the spawning of fishes, no comprehensive explanation for the variation in the distribution of spawning jack mackerel can be given at this time. It is concluded that temperature is important, but not the controlling factor in spatial-temporal distribution of spawning jack mackerel.

SURVIVAL OF THE LARVAE

The method used by Ahlstrom (1954b) to determine the survival of larvae has been retained so that interspecific comparisons might more easily be made for fish occupying the area surveyed by the California Cooperative Oceanic Fisheries Investigations. All larvae of a species were withdrawn from a station sample and measured. The measurements are grouped into size classes and adjusted by the standard haul factor (p. 250). These standardized counts are integrated over time and space (p. 251) and adjusted for growth. The products are summed for the year to give an estimate of abundance of the size class. The decline in abundance of successively larger size classes provides an estimate of survival.

REGIONAL ESTIMATES OF ABUNDANCE OF LARVAE

The regional estimates of abundance by size class for jack mackerel larvae are given in table 20 for 1952, table 21 for 1953, and table 22 for 1954. These tables are summarized in tables 23 and 24, and the annual estimates of abundance and survival are given in table 25. It will be noted that the curves shown in figure 11 derived from this table are very similar, suggesting that the number of larvae surviving a 30-day period has

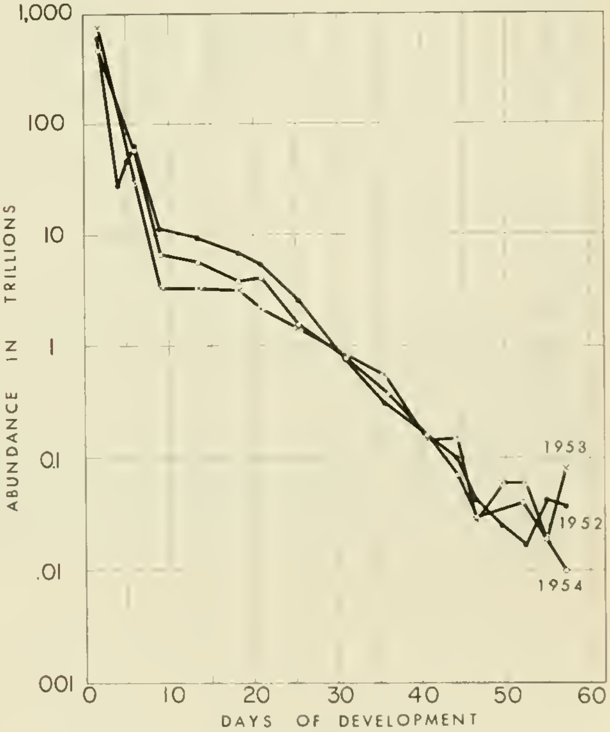


Figure 11.—Abundance curves of jack mackerel larvae to age 57 days, 1952–54.

been relatively constant. In 1952, of the 593 trillion eggs estimated to have been spawned, only 780 billion larvae are estimated to have survived at the end of 30 days. In 1953, 736 trillion eggs were estimated to have been spawned and 850 billion larvae are estimated to have survived, while in 1954, 462 trillion eggs were estimated to have been spawned with 830 billion larvae the estimated survivors at the end of the first month of life. This indicates an average survival (for the first month of life) of a little more than 1 larva per 1,000 eggs spawned.

TABLE 20.—*Regional distribution of jack mackerel larvae, by month and size class, 1952*

[In billions]

Area and month	2.0 mm.	2.5 mm.	3.0 mm.	3.5 mm.	4.0 mm.	4.5 mm.	5.0 mm.	5.75 mm.	6.75 mm.	7.75 mm.	8.75 mm.	9.75 mm.	10.75 mm.	11.75 mm.	12.75 mm.	13.75 mm.	14.75 mm.
Northern California (lines 40–77):																	
April	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
May	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
June	550	561	1, 537	29	36	38	12	0	0	0	0	0	0	0	0	0	0
July	242	1, 246	1, 541	107	57	9	48	53	0	0	0	0	0	0	0	0	0
August	42	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Total	834	1, 807	3, 078	136	93	47	60	53	0	0	0	0	0	0	0	0	0
Southern California (lines 80–93):																	
January	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
February	311	230	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
March	2, 156	3, 068	2, 334	468	258	261	103	33	0	0	0	0	0	0	0	0	0
April	134	1, 287	2, 916	1, 026	2, 337	1, 351	1, 429	409	33	12	0	0	0	0	0	0	0
May	3, 130	8, 654	8, 116	841	582	183	145	17	0	0	0	0	8	0	0	0	0
June	1, 640	2, 727	5, 355	778	1, 206	926	766	252	71	15	0	0	8	0	0	0	0
July	285	2, 145	2, 591	1, 098	391	704	668	553	235	95	7	0	0	25	0	0	0
August	307	761	1, 250	24	30	0	0	38	9	0	12	14	0	0	17	0	0
September	480	503	140	7	23	0	0	0	0	0	0	0	0	0	0	0	0
October	0	0	15	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Total	8, 443	19, 375	22, 717	4, 242	4, 827	3, 425	3, 111	1, 302	348	122	19	14	16	25	17	0	0
Northern Baja California (lines 97–107):																	
January	0	26	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
February	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
March	363	2, 825	3, 599	1, 361	425	205	15	22	0	0	0	0	0	0	0	0	0
April	7, 089	6, 478	3, 749	383	960	292	551	325	82	28	0	0	0	0	0	0	0
May	3, 374	6, 506	6, 944	577	7	168	359	70	28	11	0	8	0	0	0	0	0
June	83	510	2, 930	629	505	284	254	204	147	83	16	0	5	0	0	0	0
July	1, 962	3, 612	7, 523	2, 103	1, 241	1, 238	379	277	50	36	103	58	0	0	0	0	37
August	27	1, 284	2, 365	283	189	77	51	16	9	0	0	0	6	0	0	0	0
September	0	68	151	73	264	205	18	0	0	0	0	0	0	0	0	0	0
October	0	15	0	0	0	0	14	0	0	0	0	0	0	0	0	0	0
Total	12, 898	21, 324	27, 261	5, 409	3, 591	2, 469	1, 641	914	316	158	119	66	11	0	0	0	37
Upper central Baja California (lines 110–120):																	
February	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
March	0	0	112	236	300	421	284	99	58	0	0	0	15	0	0	0	0
April	5, 410	3, 510	5, 393	161	56	19	22	33	32	0	11	0	0	0	0	0	0
May	628	985	1, 465	634	396	338	185	138	11	17	20	0	0	0	0	0	0
June	0	258	1, 534	127	49	37	45	20	5	23	0	0	0	0	0	20	0
July	0	152	138	78	59	130	86	18	11	0	0	0	0	0	0	23	0
August	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Total	6, 038	4, 905	8, 642	1, 236	860	945	622	308	117	40	31	0	15	0	0	43	0
Lower central Baja California (lines 123–137):																	
March	0	49	48	8	34	29	0	0	0	0	0	0	0	0	0	0	0
April	0	448	1, 179	65	0	0	0	0	0	0	0	22	0	0	0	0	0
May	83	25	441	50	45	21	45	6	0	0	0	0	0	0	0	0	0
June	0	122	97	0	0	0	0	4	0	0	0	0	0	0	0	0	0
Total	83	644	1, 765	123	79	50	45	10	0	0	0	22	0	0	0	0	0
Grand total	28, 296	48, 055	63, 463	11, 146	9, 450	6, 936	5, 479	2, 587	781	320	169	102	42	25	17	43	37

The slope of the abundance curve is not constant. Survival during the first 9 days is very low but after this initial period, it is better. The inconsistency in the estimates of larvae older than 40 days is most likely due to sample variation. These estimates are made from small numbers of observations and have therefore a large error associated with them.

Although these data are in some respects quite limited, they are comparable with the survival data collected by Sette (1943) for Atlantic mackerel and Ahlstrom (1954b) for Pacific sardine.

TABLE 21.—*Regional distribution of jack mackerel larvae, by month and size class, 1953*

[In billions]

Area and month	3.0 mm.	3.5 mm.	4.0 mm.	4.5 mm.	5.0 mm.	5.75 mm.	6.75 mm.	7.75 mm.	8.75 mm.	9.75 mm.	10.75 mm.	11.75 mm.	12.75 mm.	13.75 mm.	14.75 mm.
Northern California (lines 40–77):															
June	316	66	75	0	0	0	0	201	0	0	0	0	0	0	0
July	175	51	40	40	15	17	10	0	0	0	0	0	0	0	0
August	64	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Total	555	117	115	40	15	17	10	201	0	0	0	0	0	0	0
Southern California (lines 80–93):															
February	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
March	2,846	113	11	11	0	4	50	0	0	0	0	0	18	0	0
April	1,067	515	252	126	0	0	0	0	0	33	0	0	0	0	0
May	5,017	620	426	211	55	61	0	0	0	0	0	0	0	0	0
June	2,086	125	410	362	491	360	181	57	0	0	0	0	0	0	0
July	883	114	51	315	27	261	68	0	20	22	0	0	30	0	59
August	32	0	0	0	36	19	0	0	0	0	0	0	0	0	0
September	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
October	0	0	0	0	0	0	2	0	10	0	0	0	0	0	0
Total	11,931	1,487	1,150	1,025	609	705	301	57	30	55	0	0	48	0	59
Northern Baja California (lines 97-107):															
February	2,712	274	161	17	0	0	0	41	0	0	0	0	0	0	0
March	996	223	697	971	409	69	69	11	0	10	0	0	0	0	0
April	1,512	89	87	96	87	23	17	12	0	6	0	0	0	0	0
May	1,249	188	261	346	138	155	65	0	0	0	0	0	0	0	0
June	3,621	358	280	337	488	206	208	41	62	0	7	0	0	0	0
July	213	22	70	8	18	20	6	13	0	0	0	0	0	0	0
August	0	0	0	0	0	0	20	0	0	0	0	0	0	0	0
September	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
October	151	0	64	10	46	18	20	0	6	0	0	0	0	0	0
Total	10,454	1,154	1,620	1,785	1,186	491	405	118	68	16	7	0	0	0	0
Upper central Baja California (lines 110–120):															
February	183	0	0	0	11	0	0	0	0	0	0	0	0	0	0
March	680	58	145	155	267	186	15	69	0	6	0	14	0	0	0
April	864	62	9	6	37	4	8	16	0	16	0	0	0	0	0
May	1,224	57	140	78	29	24	64	16	0	0	0	8	0	0	0
June	2,446	292	104	51	30	14	24	40	35	15	0	16	0	20	0
July	0	0	0	0	0	0	25	0	0	0	0	23	13	0	0
August	0	9	0	0	0	0	0	0	0	0	0	0	0	0	0
September	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
October	104	0	0	0	0	18	0	40	13	44	21	0	0	0	22
Total	5,501	478	398	290	374	246	136	181	48	81	21	61	13	20	22
Lower central Baja California (lines 123–137):															
May	463	16	12	8	7	0	0	0	0	0	0	0	0	0	0
June	646	60	18	20	0	9	0	0	0	0	0	0	0	0	0
July	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
October	0	0	6	0	0	0	0	0	0	0	0	0	0	0	0
Total	1,109	76	36	28	7	9	0	0	0	0	0	0	0	0	0
Grand total	29,550	3,312	3,319	3,168	2,191	1,468	852	557	146	152	28	61	61	20	81

TABLE 22.—*Regional distribution of jack mackerel larvae, by month and size class, 1954*

[In billions]

Month and area	3.0 mm.	3.5 mm.	4.0 mm.	4.5 mm.	5.0 mm.	5.75 mm.	6.75 mm.	7.75 mm.	8.75 mm.	9.75 mm.	10.75 mm.	11.75 mm.	12.75 mm.	13.75 mm.	14.75 mm.
Northern California (lines 40–77):															
May	269	0	0	0	0	0	0	0	0	0	0	0	0	0	0
June	2,061	210	150	141	108	17	0	0	0	0	0	0	0	0	0
July	578	0	222	57	0	67	116	164	97	46	0	0	41	0	0
August	0	0	0	0	0	0	53	0	0	0	0	0	0	0	0
Total	2,908	210	372	198	108	84	169	164	97	46	0	0	41	0	0
Southern California (lines 80–93):															
April	4,099	241	77	84	63	9	15	5	0	0	0	0	0	0	0
May	6,549	525	130	59	31	29	18	0	0	0	0	0	0	0	0
June	21,445	3,122	3,371	2,146	2,491	1,034	478	222	22	13	0	0	0	0	0
July	455	0	0	0	0	37	16	0	10	0	0	0	0	0	0
August	39	4	5	15	10	5	1	0	4	0	0	0	0	0	0
September	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
October	133	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Total	32,720	3,892	3,583	2,304	2,595	1,114	528	227	36	13	0	0	0	0	0
Northern Baja California (lines 97–107):															
February	175	0	0	0	0	0	0	0	0	0	0	0	0	0	0
March	2,424	185	97	371	555	85	9	6	0	0	0	0	0	0	0
April	5,022	707	353	456	278	88	45	30	10	0	0	0	0	0	0
May	4,566	428	203	102	78	38	21	16	21	0	26	0	0	0	0
June	2,704	301	303	79	194	103	42	6	0	0	0	0	0	0	0
July	741	14	17	0	0	6	7	0	0	0	0	0	0	0	0
August	61	31	18	0	9	11	0	0	0	0	5	0	0	0	10
Total	15,693	1,666	991	1,008	1,114	331	124	58	31	0	31	0	0	0	10
Upper central Baja California (lines 110–120):															
February	820	37	15	22	0	0	0	0	0	0	0	0	0	0	0
March	2,437	214	321	139	84	5	0	0	0	0	0	0	0	0	0
April	1,058	76	235	64	4	0	3	0	0	0	0	0	0	0	0
May	1,312	373	125	39	139	0	4	0	0	0	0	0	0	0	0
June	1,710	162	96	60	92	12	0	35	0	0	0	0	0	0	0
July	27	39	0	0	0	0	0	0	0	0	0	0	0	0	0
Total	7,364	901	792	324	319	17	7	35	0	0	0	0	0	0	0
Lower central Baja California (lines 123–137):															
January	198	17	10	0	0	0	0	0	0	0	0	0	0	0	0
February	0	9	0	0	0	0	0	0	0	0	0	0	0	0	0
March	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
April	270	19	0	0	6	0	0	0	0	13	0	0	0	0	0
May	70	0	0	0	8	2	5	0	0	0	0	0	0	0	0
June	74	10	0	0	0	0	0	0	0	0	0	0	0	0	0
July	0	18	0	0	0	0	0	0	0	0	0	0	0	0	0
August	0	17	0	0	0	0	0	0	0	0	0	0	0	0	0
Total	612	90	10	0	14	2	5	0	0	13	0	0	0	0	0
Grand total	59,297	6,759	5,748	3,834	4,150	1,518	833	484	164	72	31	0	41	0	10

TABLE 23.—*Regional distribution of jack mackerel larvae, by size class, 1952–54*

[In billions]

Year and region	3.0 mm.	3.5 mm.	4.0 mm.	4.5 mm.	5.0 mm.	5.75 mm.	6.75 mm.	7.75 mm.	8.75 mm.	9.75 mm.	10.75 mm.	11.75 mm.	12.75 mm.	13.75 mm.	14.75 mm.
1952:															
Northern California (lines 40–77)	3,078	136	93	47	60	53	0	0	0	0	0	0	0	0	0
Southern California (lines 80–93)	22,717	4,242	4,827	3,425	3,111	1,302	348	122	19	14	16	25	17	0	0
Northern Baja California (lines 97–107)	27,261	5,409	3,591	2,469	1,641	914	316	157	119	66	11	0	0	0	37
Upper central Baja California (lines 110–120)	8,642	1,236	860	945	622	308	117	40	31	0	15	0	0	43	0
Lower central Baja California (lines 123–137)	1,765	123	79	50	45	10	0	0	0	22	0	0	0	0	0
Total	63,463	11,146	9,450	6,936	5,479	2,587	781	319	169	102	42	25	17	43	37
1953:															
Northern California (lines 40–77)	555	117	115	40	15	17	10	201	0	0	0	0	0	0	0
Southern California (lines 80–93)	11,931	1,487	1,150	1,025	609	705	301	57	30	55	0	0	48	0	59
Northern Baja California (lines 97–107)	10,454	1,154	1,620	1,785	1,186	491	405	118	68	16	7	0	0	0	0
Upper central Baja California (lines 110–120)	5,501	478	398	290	374	246	136	181	48	81	21	61	13	20	22
Lower central Baja California (lines 123–137)	1,109	76	36	28	7	9	0	0	0	0	0	0	0	0	0
Total	29,550	3,312	3,319	3,168	2,191	1,468	852	557	146	152	28	61	61	20	81
1954:															
Northern California (lines 40–77)	2,908	210	372	198	108	84	169	164	97	46	0	0	41	0	0
Southern California (lines 80–93)	32,720	3,892	3,583	2,304	2,595	1,114	528	227	36	13	0	0	0	0	0
Northern Baja California (lines 97–107)	15,693	1,666	991	1,008	1,114	331	124	58	31	0	31	0	0	0	10
Upper central Baja California (lines 110–120)	7,364	901	792	324	319	17	7	35	0	0	0	0	0	0	0
Lower central Baja California (lines 123–137)	612	90	10	0	14	2	5	0	0	13	0	0	0	0	0
Total	59,297	6,759	5,748	3,834	4,150	1,548	833	484	164	72	31	0	41	0	10

TABLE 24.—*Percentage of each size class of jack mackerel larvae, occurring in each region, 1952–54*

Year and region	3.0 mm.	3.5 mm.	4.0 mm.	4.5 mm.	5.0 mm.	5.75 mm.	6.75 mm.	7.75 mm.	8.75 mm.	9.75 mm.	10.75 mm.	11.75 mm.	12.75 mm.	13.75 mm.	14.75 mm.
1952:															
Northern California (lines 40–77)	4.9	1.2	1.0	0.7	1.1	2.0	0	0	0	0	0	0	0	0	0
Southern California (lines 80–93)	35.8	38.0	50.9	49.4	56.7	50.2	44.8	38.1	10.9	13.7	39.0	100.0	100.0	0	0
Northern Baja California (lines 97–107)	43.1	48.6	37.8	35.6	30.0	35.2	40.5	49.4	71.0	65.1	26.7	0	0	0	100.0
Upper central Baja California (lines 110–120)	13.6	11.1	9.1	13.6	11.3	11.8	14.7	12.5	18.1	0	34.3	0	0	100.0	0
Lower central Baja California (lines 123–137)	2.8	1.1	0.8	0.7	0.8	0.4	0	0	0	21.2	0	0	0	0	0
Total	100.2	100.0	99.6	100.0	99.9	99.6	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0
1953:															
Northern California (lines 40–77)	1.8	3.5	3.5	1.3	0.7	1.1	1.2	36.1	0	0	0	0	0	0	0
Southern California (lines 80–93)	40.4	44.8	34.6	32.4	27.8	48.0	35.4	10.3	20.4	35.9	0	0	79.4	0	72.6
Northern Baja California (lines 97–107)	35.4	34.9	48.8	56.3	54.1	33.4	47.5	21.1	46.5	10.3	26.3	0	0	0	0
Upper central Baja California (lines 110–120)	18.6	14.4	11.9	9.2	17.0	16.8	15.9	32.5	32.9	53.8	73.7	100.0	20.6	100.0	27.4
Lower central Baja California (lines 123–137)	3.8	2.3	1.1	0.9	0.3	0.6	0	0	0	0	0	0	0	0	0
Total	100.0	99.9	99.9	100.1	99.9	99.9	100.0	100.0	99.8	100.0	100.0	100.0	100.0	100.0	100.0
1954:															
Northern California (lines 40–77)	4.9	3.1	6.5	5.2	2.6	5.4	20.3	34.1	59.2	64.5	0	0	100.0	0	0
Southern California (lines 80–93)	55.2	57.4	62.4	60.1	62.6	72.1	63.4	47.0	22.0	17.7	0	0	0	0	0
Northern Baja California (lines 97–107)	26.4	24.6	17.3	26.2	26.9	21.4	14.9	11.7	18.8	0	100.0	0	0	0	100.0
Upper central Baja California (lines 110–120)	12.4	13.3	13.8	8.4	7.7	1.0	0.7	7.2	0	0	0	0	0	0	0
Lower central Baja California (lines 123–137)	1.0	1.3	0.2	0	0.3	0.1	0.6	0	0	17.8	0	0	0	0	0
Total	99.9	99.7	100.2	99.9	100.1	100.0	99.9	100.0	100.0	100.0	100.0	0	100.0	0	100.0

TABLE 25.—*Annual estimates of abundance and survival of jack mackerel eggs and larvae, 1952–54*

[In billions]

Category	Duration (days)	Average age (days)	Size range (mm.)	1952		1953		1954	
				Abundance	Survival per 100,000 eggs	Abundance	Survival per 100,000 eggs	Abundance	Survival per 100,000 eggs
Eggs	3.6	1.8	----------	593,100	----------	736,100	----------	462,300	----------
Larvae:									
2.0 mm	1.0	4.1	1.90– 2.25	28,300	4,711	----------	----------	----------	----------
2.5 mm	1.0	5.1	2.26– 2.75	48,100	8,109	----------	----------	----------	----------
3.0 mm	1.0	6.1	2.76– 3.25	63,500	10,706	29,500	4,007	59,300	12,827
3.5 mm	4.8	9.0	3.26– 3.75	11,100	1,871	3,300	448	6,800	1,470
4.0 mm	4.2	13.5	3.76– 4.25	9,400	1,648	3,300	448	5,700	1,232
4.5 mm	3.7	17.4	4.26– 4.75	6,900	1,163	3,200	434	3.800	821
5.0 mm	3.3	21.0	4.76– 5.25	5,500	927	2,200	298	4,100	886
5.75 mm	5.9	25.5	5.26– 6.25	2,600	438	1,500	203	1,500	324
6.75 mm	5.0	31.0	6.26– 7.25	780	131	850	115	830	179
7.75 mm	4.3	35.7	7.26– 8.25	320	53	560	76	480	97
8.75 mm	3.8	39.4	8.26– 9.25	170	28	150	20	160	34
9.75 mm	3.5	43.3	9.26–10.25	100	16	150	20	71	15
10.75 mm	3.1	46.7	10.26–11.25	42	7	28	3	30	6
11.75 mm	2.9	49.7	11.26–12.25	25	4	60	8	----------	----------
12.75 mm	2.6	52.4	12.26–13.25	17	2	60	8	41	8
13.75 mm	2.4	54.9	13.26–14.25	43	7	20	2	----------	----------
14.75 mm	2.3	57.2	14.26–15.25	37	6	81	11	10	2

GROWTH RATE OF LARVAE

The growth rate of jack mackerel larvae was obtained by direct observation of material taken from station 70 on line 97 (97.70) during March of 1957 (Farris, 1959). Eggs were taken from the sea with a plankton net, sorted according to developmental stage, placed in jars of fresh sea water, and observed daily until they hatched. After hatching the larvae were measured daily until they died. No attempt was made to feed the fish. The measurements were averaged daily and plotted as log average length against days (fig. 12). Such a plot suggested that growth during the first 3 days was more rapid than for the next 4 days. The yolk sac was absorbed and the eyes became pigmented on the sixth day of larval life. The growth rates for the first 3 days (section A) and for the following 4 days (section B) were then compared by regression analysis (table 26), where X=days past hatching, Y=length in millimeters, $\log Y=a+bX$, s_b=standard deviation of slope, and $s_{y/x}$=standard deviation of sample points

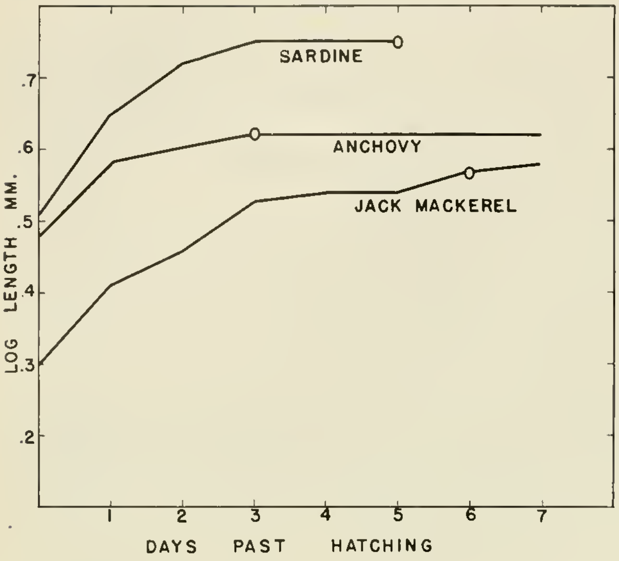


FIGURE 12.—Growth curves of jack mackerel, Pacific sardine, and northern anchovy. (Open circles indicate complete absorption of the yolk.)

from the line. The comparison of the two slopes indicated that the initial relative growth rate is about five times that of the later relative growth rate.

TABLE 26.—*Regression statistics for the relative growth rate of jack mackerel larvae*

	a	b	s_b	$s_{y/x}$	$\bar{X}$	$\bar{Y}$
Section A: days 1 through 3	0.328	0.067	0.0091	0.0616	1.3	0.614
Section B: days 4 through 8	.486	.013	.0017	.0184	3.1	.687

The relative growth rates of the other two species (Pacific sardine, *Sardinops caerulea*, and northern anchovy, *Engraulis mordax*) illustrated in figure 12 are similar to the growth rate shown for jack mackerel. In addition, the relative growth rate of the sardine as determined by direct observation ($b=0.018$) is in good agreement with the relative growth rate ($b=0.019$) determined by Ahlstrom (1954b) using an indirect method (Farris, 1959: p. 33). Ahlstrom, working with preserved material, was able to follow length-frequency modes through time.

Although growth has been described by two log curves instead of one, either would have served as well for estimating survival. The abundance of a size class is given by the following equation:

$$C=\sum_{i=1}^{n}\frac{c_i'w_it_i}{d_i}$$

where

C=estimate of total abundance of larvae of size class

c_i'=standard number of larvae belonging to the size class at the ith station

w_i=area factor proportional to area of the ith station

t_i=time factor equal to one-half the time from preceding ocupancy plus one-half the time to succeeding occupancy

d_i=duration of size category in days, i.e., the number of days used by larvae to grow from the lower-size boundary to the upper-size boundary of the size class

n=number of stations considered.

The effects of 1- and 2-phase growth on mortality estimates were compared by recomputing estimates of abundance for sardines given by Ahlstrom (1954b: p. 133). In recomputing abundance of yolk-sac larvae, the formula used was—Duration of size category (days)=

$$\frac{\log l''-\log l'}{0.081},$$

where 0.081 is the log increase in length per day of the larvae, l' is the lower boundary of the size-class interval, and l'' is the upper boundary of the size-class interval. The duration of size category for the remaining size categories of larvae is given by—

$$\frac{\log l''-\log l'}{0.018}.$$

The results of the recomputation are given in table 27 under the heading "double phase," and may be compared with Ahlstrom's figures. The slight differences in average age for given size may be due to shrinkage of the larvae upon preservation in formalin.

Since relative growth rates derived from laboratory observations on the first 5 days in the life of a sardine could be extrapolated and reconciled with field observations, it was assumed that the extrapolation could be made for jack mackerel, too.

An analysis of successive length–frequency diagrams has not been used because the time interval between successive cruises is too great for the estimation of a rapid growth rate. Secondly, any changes in the survival of larvae between cruises would influence the length frequencies; hence the changes would alter the estimation of the growth parameter and thereby alter the estimates of annual survival. A growth rate derived from direct observation has the advantage of being independent of variation in survival.

Table 27.—*Estimates of abundance of young sardine, using single phase and double phase growth curves, 1950*

[Single phase after Ahlstrom (1954b)]

Category	Size range (mm.)	Duration (days)	Average age (days)	Estimated abundance
Single phase:				
Egg	------------	3.0	1.5	285,676
Yolk-sac larvae	2.26– 4.25	3.5	4.8	11,850
Larvae:				
4.75 mm	4.26– 5.25	4.8	8.9	10,778
5.75 mm	5.26– 6.25	3.9	13.2	5,590
6.75 mm	6.26– 7.25	3.3	16.8	6,197
7.75 mm	7.26– 8.25	2.9	20.0	5,931
8.75 mm	8.26– 9.25	2.6	22.7	4,834
9.75 mm	9.26–10.25	2.3	25.1	3,738
10.75 mm	10.26–11.25	2.1	27.3	2,880
Double phase:				
Egg	------------	3.0	1.5	285,676
Yolk-sac larvae:				
3.25 mm	2.26– 4.25	1.9	3.9	21,829
4.75 mm	4.26– 5.25	5.1	7.5	10,144
Larvae:				
5.75 mm	5.26– 6.25	4.2	12.1	5,191
6.75 mm	6.26– 7.25	3.5	15.9	5,843
7.75 mm	7.26– 8.25	3.1	19.2	5,548
8.75 mm	8.26– 9.25	2.7	22.1	4,655
9.75 mm	9.26–10.25	2.4	24.7	3,582
10.75 mm	10.26–11.25	2.2	27.0	2,749

The regression statistics of section A (table 26) were used to estimate the duration of the various size categories of jack mackerel through the 3.0-mm. size class and the regression statistics of section B for all size classes thereafter. The duration of the size category (in days) through the 3.0-mm. size category is given by—

$$\frac{\log l''-\log l'}{0.067},$$

where l'' is the upper boundary of the size class, and l' is the lower boundary.

The duration of the size category (in days) for all remaining size categories is given by—

$$\frac{\log l''-\log l'}{0.013}.$$

The average age for any size category is given by summing the duration of size class for shorter size classes and adding one-half the duration of the size category under consideration. For example, the average age of the 4.5-mm. size category is obtained by summing the durations for categories, eggs through 4.0 (15.6) and adding one half of 3.7. The average age is 17.4 days.

The coincidence of the absorption of the yolk-sac and the inflection of the survival curve is tentatively interpreted as follows:

Basic mortality rates of pelagic fish eggs and yolk-sac larvae are high owing to factors intrinsic to the eggs and inherent in the species; most of those which are unfit have died before absorbing their yolk or die shortly thereafter; the survivors beyond the critical stage now survive at a higher rate because they have successfully negotiated the change in nutrition (i.e., from yolk to copepod eggs and nauplii). A more comprehensive exposition of this hypothesis is given by Farris (1960).

SOURCES OF ERROR AND BIAS IN SAMPLING LARVAE

In the section on sources of error in egg sampling, some of the more obvious sources of error and bias were examined. These same sources of error were examined in sampling procedures for larvae. In addition, the avoidance of the net by the larvae might be added as a source of error.

RETENTION OF LARVAE BY THE NETS

Incomplete retention by the net of some small size classes of larvae becomes a serious problem. Estimates of abundance were made for the 2.0- and 2.5-mm. size classes of larvae in 1952 (table 25). These estimates are lower than the estimated abundance of the 3.0-mm. size-class larvae, indicating that the smaller size classes were undersampled. Larvae less than 3.0 mm. in length, meeting the mesh head on, are able to pass through and do not appear in our collections in proportion to their true abundance. Estimates for these size classes were not made in 1953 and 1954.

Figure 4, from Ahlstrom and Ball (1954) suggests that the head depth may be 10 to 20 percent greater than the body depth at the pectoral. If this is so, the maximum depth of the 3.0-mm. larvae is greater than the maximum mesh opening of the sampling net (0.55 mm. after shrinking and 0.7 mm. before shrinking). As the larvae grow longer, their bodies grow increasingly deep and they are therefore retained within the sampling net. Evidence that larvae 3.0 mm. and longer would be retained once they are in the plankton net is given in table 28.

TABLE 28.—*Standard length and body depth at pectoral of jack mackerel larvae*

[Measurements in millimeters]

Average standard length	Average depth at pectoral
2.8[1]	0.46[1]
3.2	0.62
3.8	0.82
4.2	1.03
4.8	1.23

[1] Data from Ahlstom and Ball (1954, p. 215–216).

SAMPLING OF THE VERTICAL RANGE

The vertical distribution of larvae was examined for both the total range and quantitative diurnal differences in abundance at different depths. The data (table 29, after Ahlstrom, 1959: p. 119) indicate that almost all the larvae were found above 100 meters and that no larvae were found below 140 meters. Since net hauls are routinely made from a 140-meters depth, the net passes through the entire water column which can be expected to contain jack mackerel larvae.

The possibility of quantitative day-night differences (because of diurnal vertical migration) was analyzed by examining the vertical distribution of samples taken during the day and at night. These comparable day-night series were completed for several stations. The 2-, 8-, and 19-meter strata contain proportionally more larvae when sampled in the day than at night. The data indicate that there may be some slight tendency for the larvae to migrate to the surface during the day; however, it is more likely that there was a change in the water being sampled at station 94.80 (5403) between the day and night series. Both sardine and anchovy larvae are known to be distributed somewhat deeper in the daytime (negative phototaxis) than at night (Ahlstrom, 1959), as are many species of plankton organisms, so that a positive phototaxis would need to be better documented than is possible from our data. No definite diurnal variation in vertical distribution is evidenced.

TABLE 29.—*Standard number of jack mackerel larvae taken in day and night hauls, by depths*

[Stations in parentheses; after Ahlstrom, 1959]

Depth range (m.)	Average depth (m.)	Day hauls							Night hauls						
		Cruise 4106 (94.37)	Cruise 4106 (94.47)	Cruise 5206 (90.28)	Cruise 5305 (93.50)	Cruise 5403 (94.80)	Total larvae taken	Percent of total	Cruise 4106 (94.37)	Cruise 4106 (94.47)	Cruise 5206 (90.28)	Cruise 5305 (93.50)	Cruise 5403 (94.80)	Total larvae taken	Percent of total
2–3	2	0	0	0	0	92	92	42.8	0	0	12	0	26	38	42.7
6–10	8	0	0	2	0	86	88	40.9	0	0	13	4	0	17	19.1
16–21	19	0	0	0	0	24	24	11.2	0	4	*0	0	5	9	10.1
24–31	28	0	0	*0	0	2	2	.9	*0	*3	0	0	7	10	11.2
33–45	41	*1	*0	0	2	2	5	2.3	0	0	1	0	6	7	7.9
46–60	56	0	0	0	0	2	2	.9	0	0	0	0	8	8	9.0
63–79	72	0	0	0	0	2	2	.9	0	0	0	0	0	0	0
92–112	105	0	0	0	*0	*0	0	0	0	0	0	*0	*0	0	0
127–150	138	0	0	0	0	0	0	0	0	0	0	0	0	0	0
200–239	215	0	0	0	0	0	0	0	0	0	0	0	0	0	0
276–291	285	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Total		1	0	2	2	210	215	99.9	0	7	26	4	52	89	100.0

*Region of the thermocline.

VARIABLE DISTRIBUTION OF LARVAE

The difficulties in assessing the variability of these estimates have previously been discussed in the section on sources of error in sampling eggs. Since the proper statistical model is not known at this time, no good estimate of error can be given. It was shown in the case of eggs that for a large number of interpolations in space and time the error tended toward zero. The error of the estimates of abundance for the larvae is probably as great as the error of the estimates for egg abundance, and very likely it is even greater. This may be particularly true for the estimates of abundance of the older size categories which are based on fewer than 10 observations.

SAMPLING OF THE HORIZONTAL RANGE

It was shown that incomplete sampling of the entire range of jack mackerel spawning introduced an error of at least 21 percent of the estimated total egg population. This error appears to be reduced for the estimates of larvae. A very small proportion of the 30-day and older larvae is taken seaward of stations 90 (tables 30, 31, and 32). These tables were constructed using the standard numbers of jack mackerel larvae (6.75 mm size-class) for all stations sampled during the year. The data were grouped by 2-month intervals about selected sampling lines and further grouped to reflect the offshore-inshore distribution of the larvae as was done with the eggs (see p. 253). The data seem to indicate that almost all the 30-day-old larvae are to be found in an area bounded by line 80 on the north, line 110 on the south, stations 90 on the west, and the coast on the east. Some larvae are found both to the north and south of the main area. This area is far more restricted than that exhibited by the distribution of the eggs (see above).

Table 30.—*Relative north-south, inshore-offshore distribution of 6.75-mm. (30-day old) jack mackerel larvae, by 2-month intervals, 1952*

[Standard haul totals]

Lines	Stations			Total	Percent
	100-seaward	90–70	60-shore		
February-March:					
60	(1)	(1)	(1)	(1)	(1)
70	(1)	(1)	(1)	(1)	(1)
80	0	0	0	0	0
90	(1)	0	0	0	0
100	(1)	0	0	0	0
110	(1)	2.7	8.3	11.0	100.0
120	(1)	0	0	0	0
Total	0	2.7	8.3	11.0	100.0
Percent	0	24.5	75.5	100.0	----------
April-May:					
60	(1)	0	0	0	0
70	(1)	0	0	0	0
80	0	0	0	0	0
90	0	9.4	0	9.4	16.8
100	0	19.2	8.2	27.4	48.9
110	(1)	9.0	10.2	19.2	34.3
120	(1)	0	0	0	0
Total	0	37.6	18.4	56.0	100.0
Percent	0	67.2	32.8	100.0	----------
June-July:					
60	0	0	0	0	0
70	0	0	0	0	0
80	0	0	0	0	0
90	0	42.4	53.3	95.7	45.4
100	0	47.1	54.9	102.0	48.4
110	(1)	3.6	5.9	9.5	4.5
120	(1)	3.1	0	3.1	1.5
Total	0	96.2	114.1	210.3	99.8
Percent	0	45.7	54.3	100.0	----------

[1] Region not occupied.

Table 31.—*Relative north-south, inshore-offshore distribution of 6.75-mm. (30-day old) jack mackerel larvae, by 2-month intervals, 1953*

[Standard haul totals]

Lines	Stations			Total	Percent
	100-seaward	90–70	60-shore		
February-March:					
60	(1)	(1)	(1)	(1)	(1)
70	(1)	(1)	(1)	(1)	(1)
80	4.9	0	0	4.9	16.2
90	(1)	0	3.8	3.8	12.5
100	(1)	8.4	8.1	16.5	54.5
110	(1)	0	5.1	5.1	16.8
120	(1)	0	0	0	0
Total	4.9	8.4	17.0	30.3	100.0
Percent	16.2	27.8	56.0	100.0	----------
April-May:					
60	0	0	0	0	0
70	(1)	0	0	0	0
80	0	0	0	0	0
90	0	0	0	0	0
100	(1)	6.9	18.4	24.3	31.6
110	(1)	0	52.6	52.6	68.5
120	(1)	0	0	0	0
Total	0	5.9	71.0	76.9	100.1
Percent	0	7.7	92.3	100.0	----------
June-July:					
60	(1)	0	0	0	0
70	0	0	0	0	0
80	0	12.1	3.0	15.1	6.9
90	(1)	35.2	36.8	72.0	32.9
100	0	32.6	18.6	51.2	23.3
110	(1)	11.8	58.9	70.7	32.2
120	(1)	0	10.3	10.3	4.7
Total	0	91.7	127.6	219.3	100.0
Percent	0	41.8	58.2	100.0	----------

[1] Region not occupied.

There are several possible explanations for the relatively restricted distribution of jack mackerel larvae. Four interactions of ocean current and fish survival are discussed as possible explanations of the observed distribution.

Uniform current flow, differential survival.—In this model, it is assumed that the southerly flowing California Current has a uniform velocity, i.e., it has no eddies or countercurrents, and the larvae have a differential survival. The eggs spawned in some part of the Current will survive at a much higher rate over those deposited in other parts. Under the conditions of this model, the older larvae (survivors) would occur in regions south of the one in which they were spawned, never north of the spawning region. If the current, though of uniform velocity, is very slow, the southward displacement will be slight and therefore very hard to measure.

Uniform current flow, uniform survival.—If the California Current flowing south contained larvae which survived equally well in any part of the current, one would expect the older larvae to

TABLE 32.—*Relative north-south, inshore-offshore distribution of 6.75-mm. (30-day old) jack mackerel larvae, by 2-month intervals, 1954*

[Standard haul totals]

Lines	Stations			Total	Percent
	100-seaward	90–70	60-shore		
February–March:					
60	(1)	(1)	(1)	(1)	(1)
70	(1)	(1)	(1)	(1)	(1)
80	0	0	0	0	0
90	(1)	0	0	0	0
100	(1)	5.3	0	5.3	100.0
110	(1)	0	0	0	0
120	(1)	0	0	0	0
Total	0	5.3	0	5.3	100.0
Percent	0	100.0	0	100.0	----------
April–May:					
60	0	0	0	0	0
70	(1)	0	0	0	0
80	(1)	4.5	0	4.5	8.4
90	(1)	3.0	6.2	9.2	17.1
100	0	3.2	8.7	11.9	22.1
110	(1)	5.9	15.8	21.7	40.1
120	(1)	0	6.6	6.6	12.3
Total	0	16.6	37.3	53.9	100.0
Percent	0	30.8	69.2	100.0	----------
June–July:					
60	0	3.0	0	3.0	1.5
70	(1)	10.6	0	10.6	5.1
80	2.8	7.7	49.8	60.3	29.5
90	(1)	54.8	56.0	110.8	54.2
100	(1)	2.9	13.8	16.7	8.2
110	(1)	0	3.1	3.1	1.5
120	(1)	0	0	0	0
Total	2.8	78.9	122.7	204.4	100.0
Percent	1.4	38.5	60.1	100.0	----------

[1] Region not occupied.

occur always to the south of the spawning area. If one considers the special conditions of low current velocity and high larval mortality, a sampling problem becomes apparent. Consider: A small subarea *X* on the periphery of the spawning area contains a thousand eggs. At the end of a month, one larva has survived. Subarea *Y* in the center of the spawning area contains a million eggs. Under conditions of uniform survival a thousand larvae would survive at the end of a month. The sampler has a much better chance of obtaining larvae from subarea *Y* than from subarea *X*. The failure in obtaining month-old larvae from peripheral areas would lead to a conclusion of better survival in the center of the spawning area, though in fact, survival was uniform over the entire area.

Differential current flow, uniform survival.—Under conditions of this model, the California Current would have an average transport to the south, but some parts of the water would move faster than others, and eddy currents would be present. The larvae, although surviving at a uniform rate, would not appear to do so because of the postulated concentrating mechanisms. A high proportion of the larvae would be found in the eddies.

Differential current flow, differential survival.—Using this model, it is virtually impossible to predict the distribution of the older larvae, as that distribution depends on the special conditions of the current and survival.

Since the average flow, as determined from dynamic topography of the California Current, is slow (about 0.2 knot) and since it contains water flowing both slower and faster accompanied by eddies, no definite conclusion may be reached concerning differential survival, although survival appears to be better in some regions (table 33).

TABLE 33.—*Annual regional summary of distribution of jack mackerel eggs and month-old larvae, 1952–54*

[Survival at the end of 1 month is given for each region]

Year and region	Eggs (billions)	Percent of total	Larvae [1] (billions)	Percent of total	Survival per 100,000 eggs
1952:					
1	15,685	2.64	0	0	0
2	246,940	41.64	348	44.8	1.4
3	257,418	43.40	316	40.5	1.2
4	68,902	11.63	115	14.7	1.7
5	4,137	0.69	0	0	0
6	0	0	0	0	0
Total	593,082	100.00	779	100.0	----------
1953:					
1	9,653	1.31	10	1.2	1.0
2	185,095	25.14	301	35.4	1.6
3	353,517	48.02	405	47.5	1.1
4	176,573	23.99	136	15.9	.8
5	11,294	1.53	0	0	0
6	----------	----------	----------	----------	----------
Total	736,132	99.99	852	100.0	----------
1954:					
1	31,116	6.73	169	20.3	5.4
2	177,141	38.31	527	63.4	3.0
3	185,765	40.18	124	14.9	.7
4	49,228	10.65	6	.7	.1
5	19,088	4.13	5	.6	.3
Total	462,338	100.00	831	99.9	----------

[1] 6.75-mm. size class; estimated to be 1 month old.

AVOIDANCE OF NET

When Ahlstrom (1954b) computed the mortality of sardines, he found that a correction was necessary to account for the larvae which dodged the sampling net. He demonstrated dodging in a relative way by examining the ratio of average number of sardine larvae per night haul (when presumably the larvae cannot see the net) to the average number of larvae per day haul. When he computed the night/day ratio for each size class he found that the ratio increased with size. The

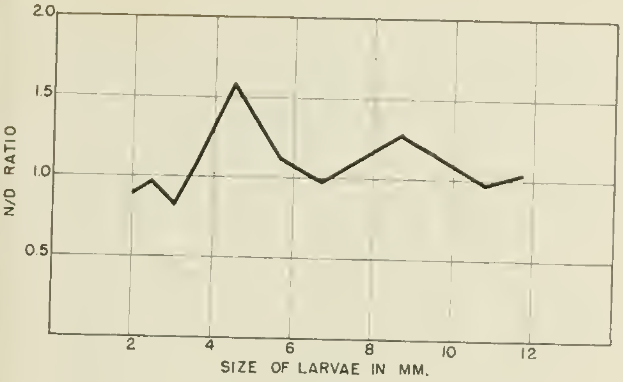


FIGURE 13.—Ratio of the average number of jack mackerel larvae per night haul to the average number taken per day (N/D), by size class, 1952–54.

implication was that as the larvae grew larger and stronger they were better able to dodge the net. This increase in ratio with size is true not only of the sardine, but also of the anchovy, the hake, the Pacific mackerel, et cetera (Ahlstrom, personal communication; Bridger, 1956).

It is, indeed, surprising to find that jack mackerel do not behave in this manner. All jack mackerel data for 3 years have been combined in figure 13. The N/D ratio for the 7.75-mm. size class has been deleted because one of the samples, which was unusually large, prevented comparison of this size class with the other size classes. A least-squares line has been fitted to the data $Y=a+bX$, where X=size in millimeters and $Y=N/D$ ratio. The regression statistics are $a=1.06$; $b=0.006$; $s_{y/x}=0.196$; $\overline{X}=6.0$; $\overline{Y}=1.10$; $s_b=0.057$.

The slope of the regression is not significantly different from zero. The interpretation placed on these data is that jack mackerel do not dodge the net despite their apparent ability to do so. The eyes are pigmented and presumably functional about the time the yolk is absorbed (at approximately 3.5 mm.), and larvae at yolk-sac absorption are capable of movement. Ahlstrom (personal communication) believes that jack mackerel larvae can swim as well as the sardine larvae.

SUMMARY

The distribution and abundance of jack mackerel eggs is described for 4 years, 1951 through 1954. The early survival of jack mackerel larvae is described for 1952, 1953, and 1954. The data were obtained from monthly cruises during which an average of 150 stations was occupied.

Jack mackerel spawned in an area bounded by the 26th parallel on the south, the 45th parallel on the north, the west coast of North America on the east, and the 150th meridian on the west. Most of the spawning occurred in a more restricted area, the boundaries of which varied from year to year. Eggs were mainly confined to the upper 40 meters of water.

Spawning usually began in February, reached a peak in May, and ceased by October. The peak of spawning in 1951, which occurred in March, is considered abnormally early.

The temperature coefficient for the rate of egg development was derived by a regression of log hours of development on temperature in degrees centigrade. Jack mackerel eggs kept under controlled temperature conditions (in an incubator) hatched at the time predicted by the derived temperature coefficient.

The estimates of egg abundance for 1951, 1952, 1953, and 1954 are 8.7×10^{14}, 5.9×10^{14}, 7.4×10^{14}, and 4.6×10^{14}, respectively.

The survival at the end of a 30-day period for 1952, 1953, and 1954 was 131, 112, and 179 larvae per 100,000 eggs spawned, respectively. The variation was considered insignificant. An increase in survival rate during the second week of larval life was noted.

The relative growth rate of jack mackerel larvae was approximated from observations on laboratory populations. The relative growth during the first 3 days is more rapid by a factor of 5 than the relative growth of the succeeding 4 days. The onset of the slower growth is correlated in time with yolk-sac absorption.

An area which is bounded by line 80 on the north, line 110 on the south, stations 90 on the west, and the coast of California and Baja California on the east has been shown to contain almost all the month-old larvae.

LITERATURE CITED

AHLSTROM, ELBERT H.
1943. Studies on the Pacific pilchard or sardine (*Sardinops caerulea*). 4. Influence of temperature on the rate of development of pilchard eggs in nature. U.S. Fish and Wildlife Service, Special Scientific Report No. 23, 26 p.
1948. A record of pilchard eggs and larvae collected during surveys made in 1939 to 1941. U.S. Fish

and Wildlife Service, Special Scientific Report No. 54, 76 p.

1953. Pilchard eggs and larvae and other fish larvae, Pacific coast—1951. U.S. Fish and Wildlife Service, Special Scientific Report: Fisheries No. 102, 55 p.

1954a. Pacific sardine (pilchard) eggs and larvae and other fish larvae, Pacific coast—1952. U.S. Fish and Wildlife Service, Special Scientific Report: Fisheries No. 123, 76 p.

1954b. Distribution and abundance of egg and larval populations of the Pacific sardine. U.S. Fish and Wildlife Service, Fishery Bulletin No. 93, vol. 56, p. 83–140.

1956. Eggs and larvae of anchovy, jack mackerel, and Pacific mackerel. Progress report of the California Cooperative Oceanic Fisheries Investigations, 1 April 1955 to 30 June 1956, p. 33–42. Sacramento, State Printer.

1959. Vertical distribution of pelagic fish eggs and larvae off California and Baja California. U.S. Fish and Wildlife Service, Fishery Bulletin No. 161, vol. 60, p. 107–146.

Ahlstrom, Elbert H., and Orville P. Ball.

1954. Description of eggs and larvae of the jack mackerel (*Trachurus symmetricus*) and distribution and abundance of larvae in 1950 and 1951. U.S. Fish and Wildlife Service, Fishery Bulletin No. 97, vol. 56, p. 209–245.

Ahlstrom, Elbert H., and David Kramer.

1955. Pacific sardine (pilchard) eggs and larvae and other fish larvae, Pacific coast—1953. U.S. Fish and Wildlife Service, Special Scientific Report: Fisheries No. 155, 74 p.

1956. Sardine eggs and larvae and other fish larvae, Pacific coast—1954. U.S. Fish and Wildlife Service, Special Scientific Report: Fisheries No. 186, 79 p.

1957. Sardine eggs and larvae and other fish larvae, Pacific coast—1955. U.S. Fish and Wildlife Service, Special Scientific Report: Fisheries No. 225, 90 p.

Barnhart, Percy Spencer.

1936. Marine fishes of southern California. University of California Press, Berkeley, California, 209 p.

Bridger, J. P.

1956. On day and night variation in catches of fish larvae. Journal du Conseil, International pour l'Exploration de la Mer, vol. 22, no. 1, p. 42–57.

California Marine Research Committee.

1950. California Cooperative Sardine Research Program, Progress Report—1950. Sacramento, State Printer, 54 p.

1952. California Cooperative Sardine Research Program, Progress Report—1 January 1951 to 30 June 1952. Sacramento, State Printer, 51 p.

1953. Progress Report, California Cooperative Oceanic Fisheries Investigations, 1 July 1952–30 June 1953. Sacramento, State Printer, 44 p.

1955. Progress Report, California Cooperative Oceanic Fisheries Investigations, 1 July 1953–31 March 1955. Sacramento, State Printer, 52 p.

1956. Progress Report, California Cooperative Oceanic Fisheries Investigations, 1 April 1955–30 June 1956. Sacramento, State Printer, 44 p.

Clothier, Charles R., and Edward C. Greenhood.

1956. Jack mackerel and sardine yield per area from California waters, 1946–47 through 1954–55. California Department of Fish and Game, Fish Bulletin No. 102, p. 7–16.

Farris, David A.

1958. Jack mackerel eggs—Pacific coast, 1951–1954. U.S. Fish and Wildlife Service, Special Scientific Report: Fisheries No. 263, 44 p.

1959. A change in the early growth rate of four larval marine fishes. Limnology and Oceanography, vol. 4, no. 1, p. 29–36.

1960. The effect of three different types of growth curves on estimates of larval fish survival. Journal du Conseil International pour l'Exploration de la Mer, vol. 25, no. 3, p. 294–306.

Fitch, John E.

1956. Jack mackerel. Progress Report of the California Cooperative Oceanic Fisheries Investigations—1 April 1955 to 30 June 1956. Sacramento, State Printer, p. 27–28.

Fowler, Henry W.

1944. The fishes: in the results of the fifth George Vanderbilt expedition (1941). Academy of Natural Science of Philadelphia, Monograph No. 6, p. 57–583.

Gamulin, T., and P. J. Hure.

1955. Contribution a la Connaissance de l'Ecologie de la Ponte de la Sardine (*Sardina pilchardus* Walb.) Dans l'Adriatique. Acta Adriatica, Institut za Oceanographiju i Ribarstvo Split FNR Jugoslavija, vol. 7, no. 8, 23 p.

Roedel, Phil M.

1949. Jack mackerel. *In* The commercial fish catch of California for the year 1947 with a historical review 1916–1947. California Department of Fish and Game, Fish Bulletin No. 74, 267 p.

Scofield, W. L.

1951. Purse seines and other roundhaul nets in California. California Department of Fish and Game, Fish Bulletin No. 81, 83 p.

Scripps Institution of Oceanography and U.S. Fish and Wildlife Service.

1952. Station positions of the California Cooperative Sardine Research Program. Scripps Institution of Oceanography, La Jolla, California, SIO Reference 52–04, 5 p.

Sette, Oscar Elton.

1943. Biology of the Atlantic mackerel (*Scomber scombrus*) of North America. Part I: Early life history, including the growth, drift, and mortality of the egg and larval populations. U.S. Fish and Wildlife Service, Fishery Bulletin No. 38, vol. 50, p. 149–237.

Sette, Oscar E., and Elbert H. Ahlstrom.
1948. Estimation of abundance of the eggs of the Pacific pilchard (*Sardinops caerulea*) off southern California during 1940–41. Journal Marine Research, vol. 7, no. 3, p. 511–542.

South Pacific Fishery Investigations.
1952. Zooplankton volumes off the Pacific coast, 1951. U.S. Fish and Wildlife Service, Special Scientific Report: Fisheries No. 73, 37 p.
1953. Zooplankton volumes off the Pacific coast, 1952. U.S. Fish and Wildlife Service, Special Scientific Report: Fisheries No. 100, 41 p.
1954. Zooplankton volumes off the Pacific coast, 1953. U.S. Fish and Wildlife Service, Special Scientific Report: Fisheries No. 132, 38 p.
1955. Zooplankton volumes off the Pacific coast, 1954. U.S. Fish and Wildlife Service, Special Scientific Report: Fisheries No. 161, 35 p.

Turner, C. Donnell.
1948. General endocrinology. W. B. Saunders Co., Philadelphia and London, 604 p.

Walford, Lionel A.
1948. The case for studying normal patterns in fishery biology. Journal Marine Research, vol. 7, no. 3, p. 505–510.

APPENDIX

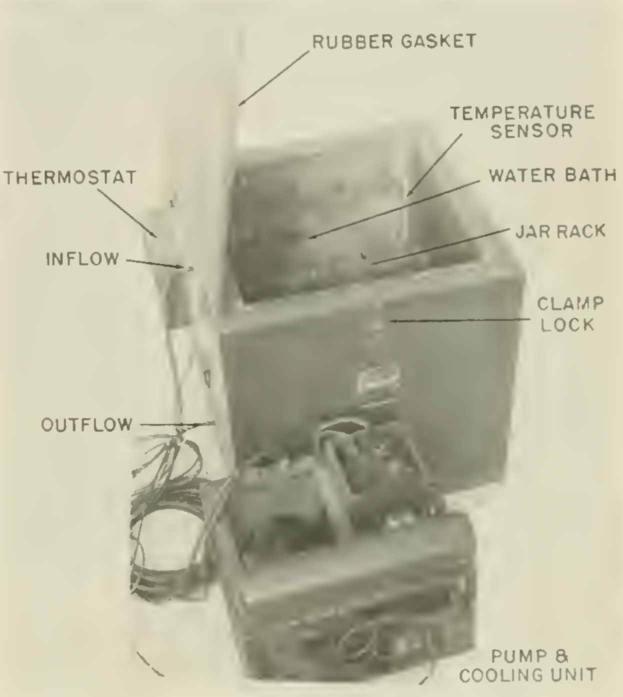
A. FISH EGG INCUBATOR

Description

When estimating the total abundance of pelagic fish eggs it is necessary to know the rate of development. Since this parameter varies with temperature it has been customary in the past to compute a regression of log hours of development against temperature in tenths of a degree centigrade. This indirect method, while very accurate, is extremely laborious and time consuming. A more direct method was desired, and with this need in mind, an incubator was designed for use at sea.

Since most of the biological material is taken well offshore, and since hatching times are relatively short, it is necessary to work at sea. Some of the many technical problems that are peculiar to sea work and their solutions are described here.

The pitch and roll of ships cause delicate equipment to be damaged quite easily, and the need for sturdy construction is readily apparent. Instruments such as this one should be portable, since they have a limited use and cannot be left aboard research vessels indefinitely. A compromise between sturdy construction and portability of an egg incubator was effected by resorting to a double-box construction, using marine plywood. The temperature-sensing and temperature-control devices were of a mechanical nature. A heavy duty, stainless steel sensing element enclosing a mercury column was employed. The mercury column activated a mechanical linkage in the thermostat, which in turn opened and closed an electrical switch. The circulating pump and cooling device were remote from the incubator itself, but connected by garden hoses (appendix fig. 1). The separation of units contributed to the portability of the instrument.



Appendix Figure 1.—Fish egg incubator.

Corrosion from the salt air which attacks most metals was controlled by using a synthetic resin paint on all exposed parts of the incubator. Other structures were concealed in corrosion resistant housings.

Temperature control (± 0.2° C. of selected temperature) was obtained by using the main water mass in the water bath as a heat reservoir. As the water mass warmed, the change in temperature was recorded by the sensing element and the water routed through the cooling mechanism. It was believed that temperature changes in the incubation chambers were small, because the main water mass was so large, by comparison, that a large amount of heat would have to be transferred before any appreciable temperature change in the incubation chambers would occur.

The eggs were incubated in pint or quart mason fruit jars. The pint jars had glass tops held in place by a spring clamp; the quart jars were wide-mouthed and equipped with plastic lids.

Procedure for use

While the vessel is still at the dock, the incubator and cooling mechanism are secured to the deck. The water bath is filled with fresh water (which causes less corrosion in the cooling system than salt water) and the circulating and cooling motors are started. Operability of the thermostat is checked.

Once the vessel is in the collecting area, the thermostat is set so that the water in the water bath assumes the same temperature as the sea. Later on, at the time the biological sample is received, a bathythermograph reading is taken and the thermostat adjusted. The fruit jars are filled with sea water from the area and the samples placed in them. A small air space is left at the top of the jars to aid aeration of the sample. The jars are then placed in the jar rack and locked into place. From then on the operation is automatic, although temperature readings should be taken frequently to assure that the incubator is operating properly.

General specifications

The outside dimensions of the incubator were 32 inches by 32 inches by 35 inches deep. The inside dimensions, the perimeter of the water bath, were 26 inches by 26 inches by 26 inches. Both the inside and outside boxes were made of ⅝-inch marine plywood fastened together with brass screws. The space between the boxes was filled with an insulating material. The inside box was lined with copper sheeting that had been soldered at the joints and was therefore watertight. The jar rack also was made of copper. The individual chambers of the bottle rack were 4 inches square and accommodated either pint or quart wide-mouthed jars.

The copper lining was pierced by three holes: one for inflowing water, one for outflowing water, and one for the temperature-sensing element.

The lid was fastened by two heavy metal strap hinges and three clamp locks. A sponge-rubber gasket prevented leakage.

The water in the water bath was circulated by a Jabsco pump and cooled by a Temprite cooler. The temperature control was maintained by a Partlow thermostat. Two ¼-inch plastic garden hoses with brass fittings connected the pump and cooler with the water bath. All exposed surfaces were painted with green plastic paint.

B. STAGING SCHEME OF JACK MACKEREL EGGS

Stage I.—Unfertilized eggs or fertilized eggs before cell division.

Stage II.—Begins when the first cell becomes visible on the yoke and ends at the completion of blastodisk formation (at about the 256-cell stage).

Stage III.—Starts at the completion of blastodisk formation and terminates when the germ ring has migrated to its greatest diameter (half-way up the egg).

Stage IV.—Begins as the germ ring moves upward over the greatest diameter and ends when the germ ring lies over the oil globule, prior to blastopore closure.

Stage V.—Begins at blastopore closure and terminates when the tail bud starts to separate from the yolk.

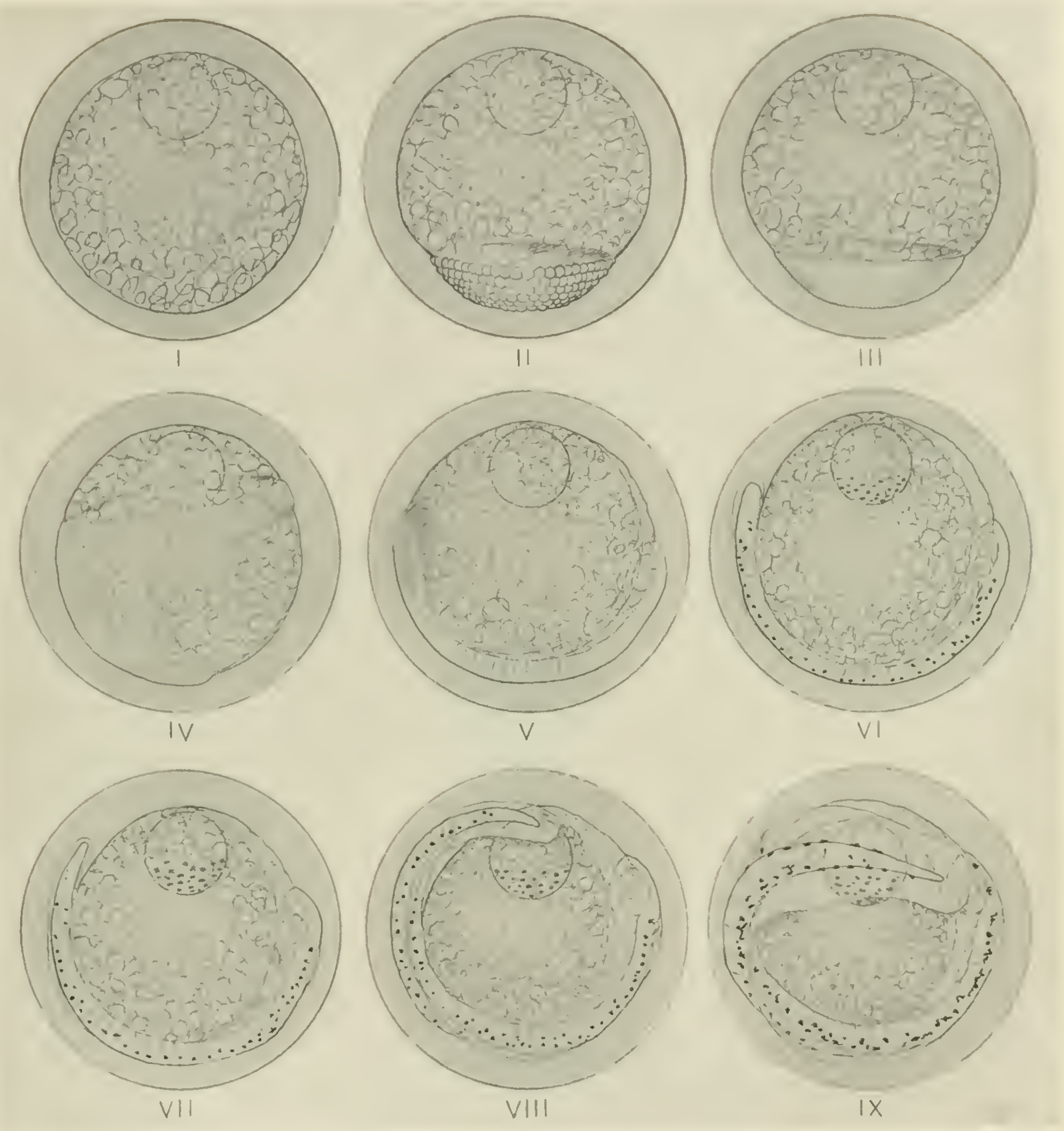
Stage VI.—Begins when the tail bud becomes free of the yolk and ends when the caudal one-eighth of the body is free of the yolk.

Stage VII.—Begins when the caudal one-eighth of the body is free of the yolk and ends when the caudal one-quarter of the body is free of the yolk. A finfold is visible.

Stage VIII.—Begins when the caudal one-quarter of the body is free of the yolk and the tip of the tail approaches the chin. The tail portion of the embryo begins to rotate out of the embryonic plane and the finfold is moderately wide.

Stage IX.—This stage is characterized by the tip of the tail laterally approaching the head. The oil globule comes to lie in the anteroventral portion of the yolk sac. The finfold is wide and fully formed. This stage terminates when the embryo hatches.

Disintegrate.—Includes all jack mackerel eggs whose internal structure is such that staging is impossible.



Appendix Figure 2.—Stages of jack mackerel egg development.

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DISTRIBUTION AND ABUNDANCE OF SKIPJACK IN THE HAWAII FISHERY, 1952–53

By HERBERT H. SHIPPEN

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ABSTRACT

Commercial catch records of the Hawaii skipjack fishery for 1952 (a poor year) and 1953 (a good year) are summarized by area and time of catch and by size composition. A unit of fishing effort and its appropriateness are discussed. Geographical distribution of the catch and effort is determined and the two years are compared. Movements of skipjack throughout the fishery are analyzed. The usefulness of the raw catch and the catch per unit of effort as indexes of abundance are considered, and some conjectures as to the nature of the population supporting the fishery are offered.

DISTRIBUTION AND ABUNDANCE OF SKIPJACK IN THE HAWAII FISHERY, 1952–53

By **Herbert H. Shippen**, *Fishery Research Biologist,*
Bureau of Commercial Fisheries

A study of the environmental factors that may influence the availability of the skipjack (*Katsuwonus pelamis*) to the Hawaii fishery was begun by the staff of the U.S. Fish and Wildlife Service Biological Laboratory (Honolulu, Hawaii). Because the index of availability is to be based on records of commercial skipjack landings, an analysis of these records is an essential part of this study.

HAWAII SKIPJACK FISHERY

The skipjack, or aku, is the most important commercial species of fish in Hawaii, both in terms of quantity landed and dollar value. The 11 million pounds caught and sold for $1,260,000 in 1956 constituted about 70 percent of the total catch of marine species and 40 percent of the value received by Hawaii fishermen during that year. Most of the catch is canned, but a small amount, estimated at less than 10 percent, is sold fresh.

June (1951) and Yamashita (1958) have described the fishery in some detail. Since World War II, the skipjack fleet has consisted of approximately 15 to 20 sampans based in Honolulu, with a few boats based at the islands of Kauai, Maui, and Hawaii. A sampan usually carries a crew of 8 to 15 men. The fishermen rely on the presence of flocks of wild birds to locate skipjack schools. The fish are caught on pole-and-line after being attracted to the boat by chumming with live bait.

The fishery is seasonal with large catches generally occurring in the summer and small catches in the winter months. Catches have fluctuated widely in recent years (fig. 1). The skipjack taken weigh from 2 to 30 pounds. The most sought after size is the 17- to 22-pound fish, known to the fishermen as "season fish." Brock (1954, p. 96) estimates these to be either in their second or third year of life. The reason for the seasonal fluctuation in the catch appears to be the migration of season fish into and out of the area of the fishery, but the direction and significance of this migration in the life history of the species are largely unknown.

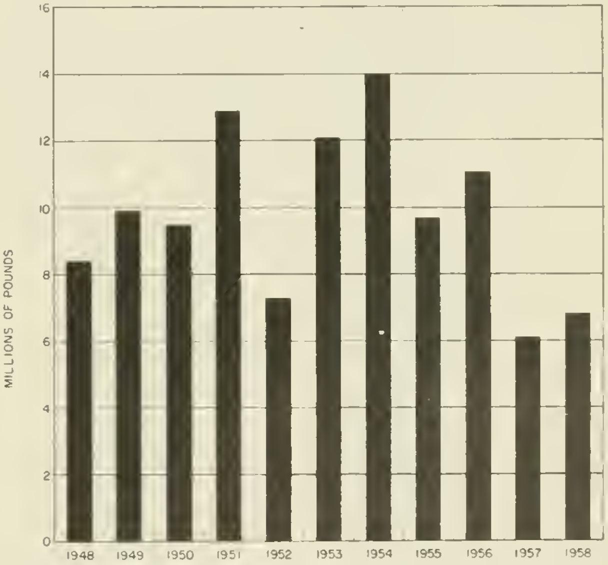


Figure 1.—Annual Hawaii skipjack catch, 1948–58.

PURPOSES OF THIS STUDY

The purposes of this study are (1) to examine the raw catch data and the catch per unit of effort as measures of the apparent abundance of skipjack; (2) to search the data for differences between good and poor years in the fishery; (3) to study movements of skipjack within the fishery during the course of the season; (4) to examine the distribution of pounds of skipjack caught, catch per unit of effort, total effort, and size composition of the catch throughout the fishery.

Note.—Approved for publication February 24, 1961. Fishery Bulletin 195.

I wish to thank the staff of the Hawaii Division of Fish and Game who collected the fish-catch reports that form the basis of this study. Vernon E. Brock and Tamotsu Shimizu made their data available for study. Additional information was received from Saul Price of the U.S. Weather Bureau who furnished the data on small craft warnings. Peter Wilson of Hawaiian Tuna Packers, Ltd., was instrumental in obtaining the logbooks from two fishing sampans; and Dr. Robert Riffenburgh suggested certain useful statistical procedures.

UTILIZATION OF DATA

The fish-catch reports (fig. 2), completed by the fishermen, were used in this study. Items in these reports are treated as follows:

Time of catch.—The interval from the beginning of 1952 through 1953 was divided into biweekly periods (table 1). Catch reports were grouped by periods according to date of landing.

TABLE 1.—*Biweekly periods in 1952 and 1953*

Period	1952	1953
1	Jan. 1-12	Dec. 28-Jan. 10.
2	Jan. 13-26	Jan. 11-24.
3	Jan. 27-Feb. 9	Jan. 25-Feb. 7.
4	Feb. 10-23	Feb. 8-21.
5	Feb. 24-Mar. 8	Feb. 22-Mar. 7
6	Mar. 9-22	Mar. 8-21.
7	Mar. 23-April 5	Mar. 22-April 4.
8	April 6-19	April 5-18.
9	April 20-May 3	April 19-May 2.
10	May 4-17	May 3-16.
11	May 18-31	May 17-30.
12	June 1-14	May 31-June 13.
13	June 15-28	June 14-27.
14	June 29-July 12	June 28-July 11.
15	July 13-26	July 12-25.
16	July 27-Aug. 9	July 26-Aug. 8.
17	Aug. 10-23	Aug. 9-22.
18	Aug. 24-Sept. 6	Aug. 23-Sept. 5.
19	Sept. 7-20	Sept. 6-19.
20	Sept. 21-Oct. 4	Sept. 20-Oct. 3.
21	Oct. 5-18	Oct. 4-17.
22	Oct. 19-Nov. 1	Oct. 18-31.
23	Nov. 2-15	Nov. 1-14.
24	Nov. 16-29	Nov. 15-28.
25	Nov. 30-Dec. 13	Nov. 29-Dec. 12.
26	Dec. 14-27	Dec. 13-26.

Area of catch.—The catch reports were sorted and reported according to statistical area (fig. 3). For reasons discussed under Sources of Error, the statistical areas have been summarized in terms of zones and regions (fig. 4).

Pounds caught.—This figure was used exactly as recorded in the catch reports.

Average size of skipjack caught.—The total weight was divided by the estimated number caught to arrive at the average weight per fish in the catch. Catches were then classified according to the following categories: (1) small fish (average weight 10 pounds or less), (2) large fish (average weight greater than 10 pounds), or (3) catches for which no size estimate was possible, because the number of fish caught was omitted from the report.

Estimate of total number of skipjack caught in each size group.—A simple proportion, utilizing the known weights and numbers, was used to estimate the numbers of small and large skipjack in the total catch. For example, if the summary of data from the fish-catch reports for a particular region and period yields the following information:

Weight and number of fish	Small skipjack	Large skipjack	No size data	Total
Pounds	30,000	50,000	40,000	120,000
Number	6,000	2,500	[1]	[1]

[1] Unknown.

then, the estimated total number of small skipjack caught is $\frac{(6{,}000)\cdot(120{,}000)}{80{,}000}=9{,}000$, and the estimated total number of large skipjack caught is $\frac{(2{,}500)\cdot(120{,}000)}{80{,}000}=3{,}750$.

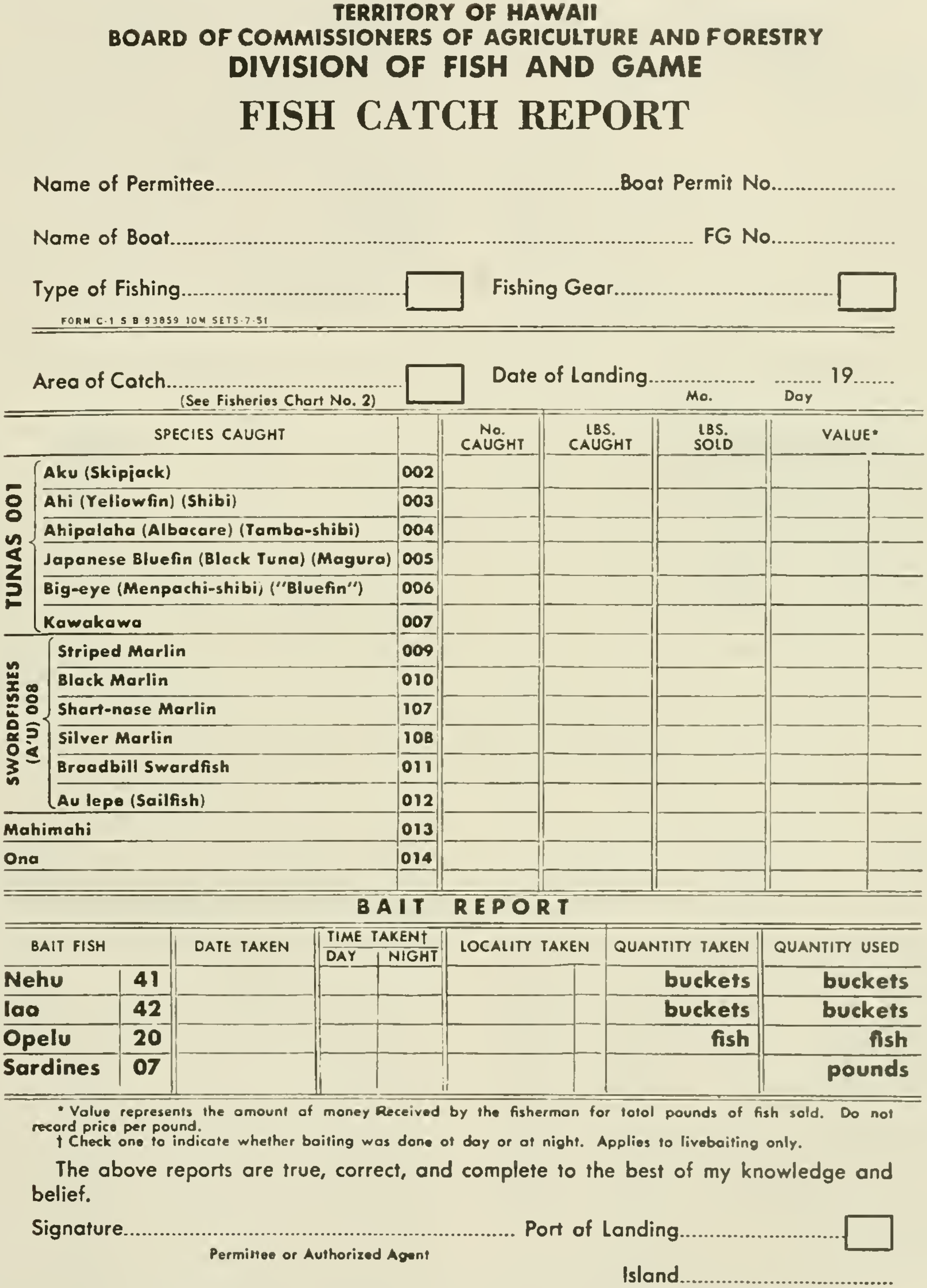
Unusable fish-catch reports.—A small number of reports was set aside and not used, except to accumulate gross totals of pounds caught. If a report fell into one or more of the following categories, it was classified as unusable: (*a*) no statistical area was given on catch report, or area number given did not appear on Division of Fish and Game Chart (fig. 3); (*b*) several statistical area numbers were given so that assignment of the catch to any single zone or region was impossible; (*c*) several trips were apparently grouped on one catch report so that estimates of fishing effort would be erroneous.

All other reports were considered usable.

CHOICE OF UNIT OF FISHING EFFORT

The fish-catch report gives no direct information on the amount of effort. There are no data to indicate the number of fishermen making the catch, the time in terms of scouting and fishing, the number of unreported trips with no catch, or any of the other factors which might be pertinent. The fish-catch reports provide, insofar as the determination of effort is concerned, a listing of dates on which fish were unloaded from the vessel. It is from this list, and other data, that fishing effort was estimated.

Each usable catch report was assumed to describe the results of a single trip of the vessel. Each boat has an official number-of-crew, which is reported to the U.S. Customs (Yamashita, 1958, table A-1). This figure, a constant for each vessel, was assigned as a weight to each usable catch report to represent the amount of effort expended in



TERRITORY OF HAWAII
BOARD OF COMMISSIONERS OF AGRICULTURE AND FORESTRY
DIVISION OF FISH AND GAME

FISH CATCH REPORT

Name of Permittee...Boat Permit No....................

Name of Boat...FG No....................

Type of Fishing.................................☐ Fishing Gear.................................☐

FORM C-1 S B 93859 10M SETS-7-51

Area of Catch.................................☐ Date of Landing.................. .... 19......
(See Fisheries Chart No. 2) Mo. Day

SPECIES CAUGHT		No. CAUGHT	LBS. CAUGHT	LBS. SOLD	VALUE*	
TUNAS 001 — Aku (Skipjack)	002					
Ahi (Yellowfin) (Shibi)	003					
Ahipalaha (Albacore) (Tamba-shibi)	004					
Japanese Bluefin (Black Tuna) (Magura)	005					
Big-eye (Menpachi-shibi) ("Bluefin")	006					
Kawakawa	007					
SWORDFISHES (A'U) 008 — Striped Marlin	009					
Black Marlin	010					
Short-nose Marlin	107					
Silver Marlin	108					
Broadbill Swordfish	011					
Au lepe (Sailfish)	012					
Mahimahi	013					
Ono	014					

BAIT REPORT

BAIT FISH		DATE TAKEN	TIME TAKEN† DAY	TIME TAKEN† NIGHT	LOCALITY TAKEN	QUANTITY TAKEN	QUANTITY USED
Nehu	41					buckets	buckets
Iao	42					buckets	buckets
Opelu	20					fish	fish
Sardines	07						pounds

* Value represents the amount of money Received by the fisherman for total pounds of fish sold. Do not record price per pound.

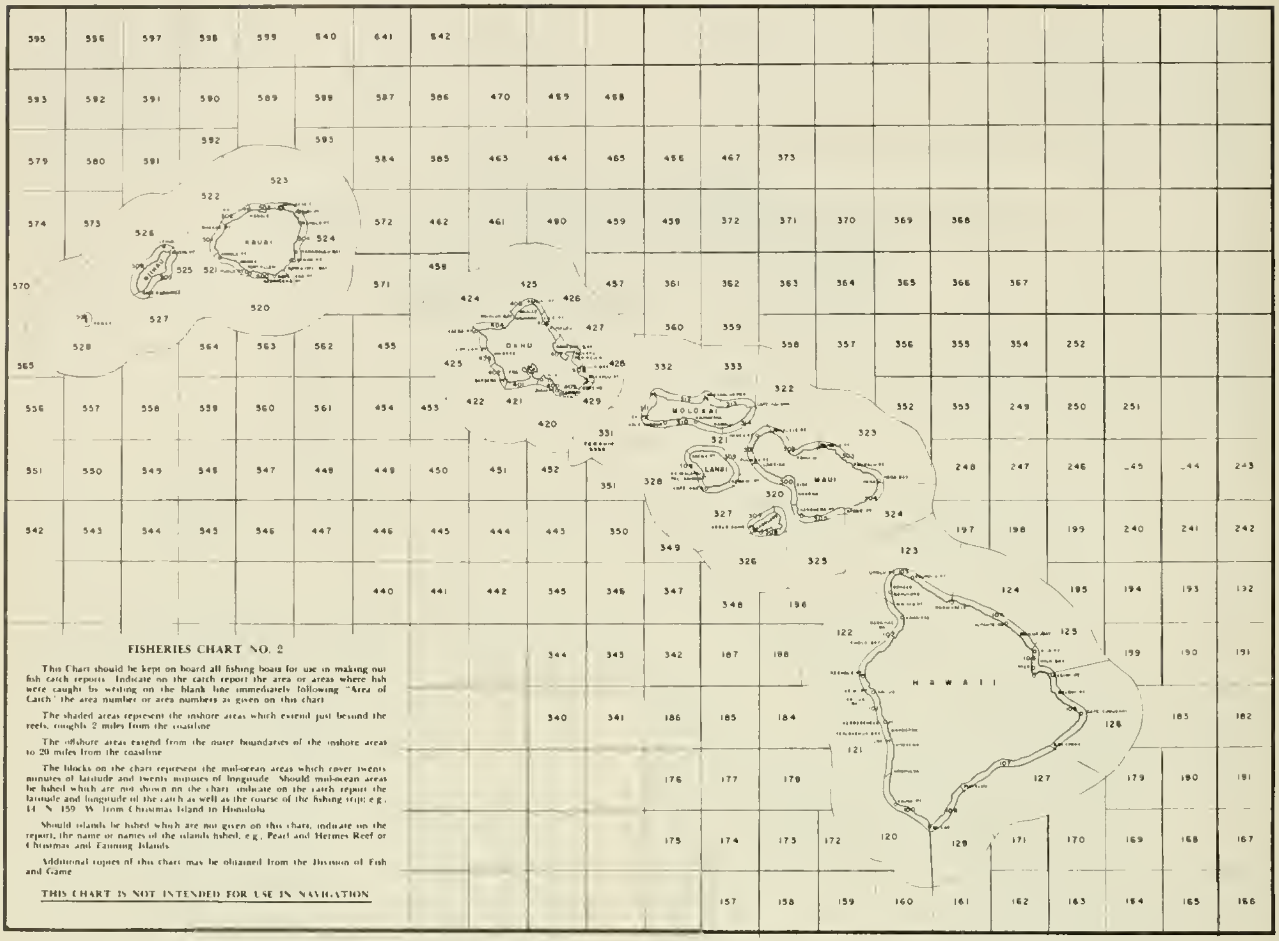
† Check one to indicate whether baiting was done at day or at night. Applies to livebaiting only.

The above reports are true, correct, and complete to the best of my knowledge and belief.

Signature.. Port of Landing..............................☐
Permittee or Authorized Agent

Island......................................

FIGURE 2.—Hawaii Division of Fish and Game, Fish Catch Report (1950–54).



FISHERIES CHART NO. 2

This Chart should be kept on board all fishing boats for use in making out fish catch reports. Indicate on the catch report the area or areas where fish were caught by writing on the blank line immediately following "Area of Catch" the area number or area numbers as given on this chart.

The shaded areas represent the inshore areas which extend just beyond the reefs, roughly 2 miles from the coastline.

The offshore areas extend from the outer boundaries of the inshore areas to 20 miles from the coastline.

The blocks on the chart represent the mid-ocean areas which cover twenty minutes of latitude and twenty minutes of longitude. Should mid-ocean areas be fished which are not shown on the chart, indicate on the catch report the latitude and longitude of the catch as well as the course of the fishing trip; e.g., 14 N 159 W from Christmas Island to Honolulu.

Should islands be fished which are not given on this chart, indicate on the report, the name or names of the islands fished, e.g., Pearl and Hermes Reef or Christmas and Fanning Islands.

Additional copies of this chart may be obtained from the Division of Fish and Game.

THIS CHART IS NOT INTENDED FOR USE IN NAVIGATION

FIGURE 3.—Hawaii Division of Fish and Game, Fisheries Chart No. 2, Statistical Areas.

TABLE 2.—*Fishing effort in 1952 and 1953 for two Honolulu-based skipjack boats*

1	2	3	4	5	6	7	8	9	10	11
Boat and period	Number biweekly periods with fishing	Number trips	Number productive trips	Number non-productive trips	Percent non-productive trips	Average number trips per biweekly period	Number days fishing (includes scouting)	Average number days fishing per biweekly period	Average number trips per days fishing	Average number productive trips per days fishing
BOAT *A* (*1952*)										
Jan. 1-May 31; Oct. 5-Dec. 27	9	42	37	5	12	4.7	51	5.7	0.82	0.73
June 1-Oct. 4	9	61	56	5	8	6.8	66	7.3	.92	.85
Jan. 1-Dec. 27, 1952	18	103	93	10	10	5.7	117	6.5	.88	.79
BOAT *A* (*1953*)										
Dec. 28, 1952-May 30, Oct. 4-Dec. 26	15	82	74	8	10	5.5	85	5.7	.96	.87
May 31-Oct. 3	9	58	55	3	5	6.4	59	6.6	.98	.93
Dec. 28, 1952-Dec. 26, 1953	24	140	129	11	8	5.8	144	6.0	.97	.90
BOAT *B* (*1952*)										
Jan. 1-May 31; Oct. 5-Dec. 27	11	29	22	7	24	2.6	55	5.0	.53	.40
June 1-Oct. 4	9	33	31	2	6	3.7	55	6.1	.60	.56
Jan. 1-Dec. 27, 1952	20	62	53	9	14	3.1	110	5.5	.56	.48
BOAT *B* (*1953*)										
Dec. 28-May 30; Oct. 4-Dec. 26	16	69	60	9	13	4.3	91	5.7	.76	.66
May 31-Oct. 3	9	50	47	3	6	5.6	65	7.2	.77	.72
Dec. 28, 1952-Dec. 26, 1953	25	119	107	12	10	4.8	156	6.2	.76	.69

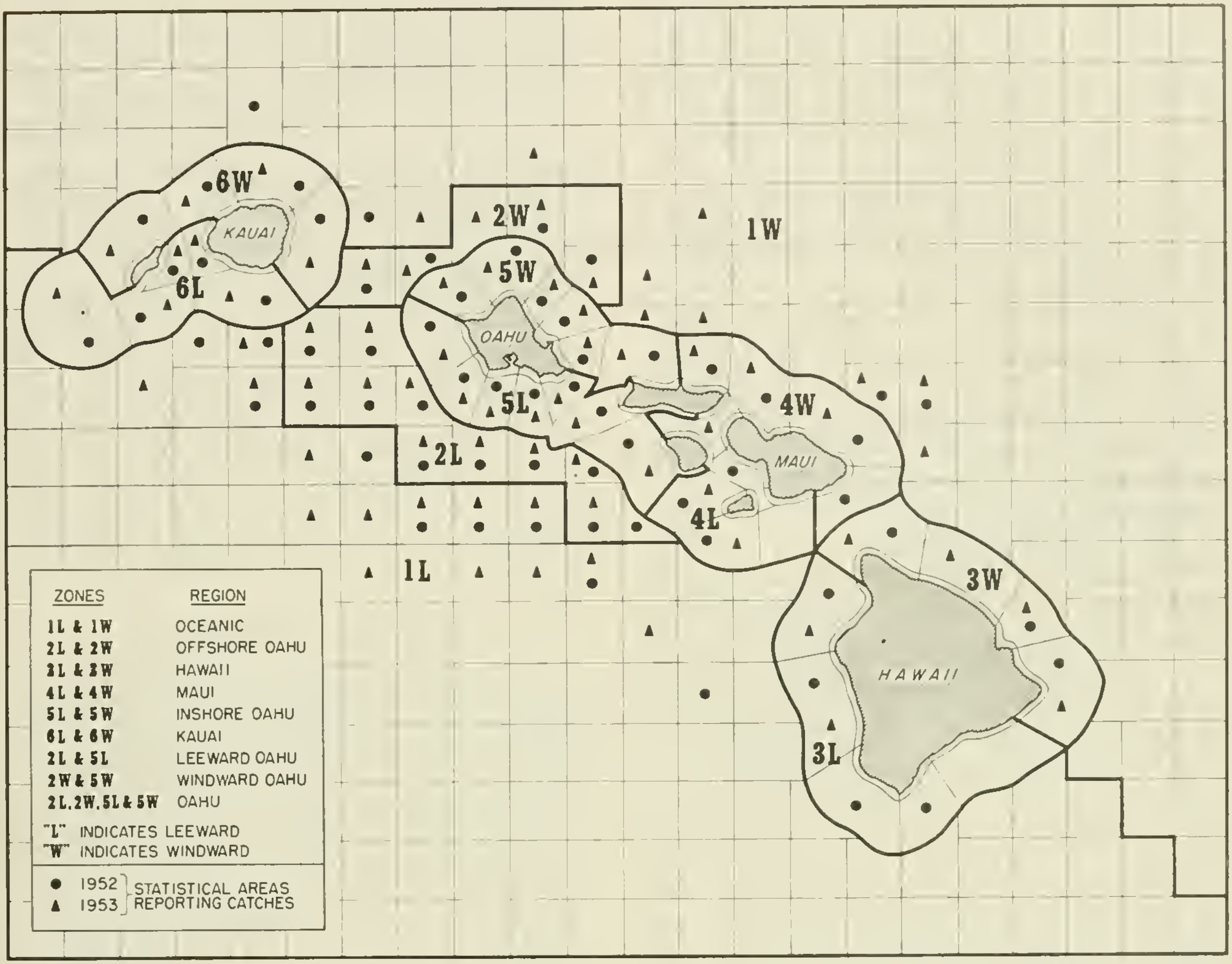


FIGURE 4.—Hawaii skipjack fishery fishing zones and regions and the extent of fishing in 1952 and 1953.

making the catch. The number of fishermen is used as a factor in the computation of fishing effort because it seems reasonable that in pole-and-line fishing the efficiency of a vessel is more or less directly related to the number of men hooking fish. No adjustments were made for differences in trip time or for deviations from the official number of fishermen. Inasmuch as a fish-catch report is required only if fish are caught, the unit of effort employed in this study is the productive fisherman-trip. Thus, if a vessel with a registered crew of 10 men reported a catch of 20,000 pounds, the effort is considered to be 10 units and the catch per unit of effort is 2,000 pounds. If two or more catch reports were combined, the sum of the catches was divided by the sum of the effort to obtain the catch per unit of effort.

To gain some knowledge of the reliability of the productive trip as a factor in the unit of effort, the logbooks of two Honolulu-based skipjack fishing sampans were analyzed to determine the ratio of productive trips to the actual number of days spent fishing; i.e., the time spent in scouting for and catching skipjack. The results of this analysis appear in table 2. Boat *A* is typical of the fleet as a whole in that it makes frequent trips of seldom more than a single day. Boat *B*, on the other hand, is probably the most atypical in the fleet since it ventures far afield and may remain at sea for as many as 4 days, especially when skipjack are relatively scarce. The differences between the two boats are apparent in the number of trips per biweekly period (col. 7) and the number of trips per day's fishing (col. 10).

Each year is divided into the more productive and less productive parts; for convenience these are called summer and winter, respectively (rows 1 and 2 for each boat and year). The number of trips per biweekly period (col. 7) and number of day's fishing per biweekly period (col. 9) are greater during summer, but the ratio of trips to day's fishing (col. 10) is not markedly different in the two seasons, although trips are somewhat longer in winter.

Nonproductive trips (col. 5) occur with greater frequency (col. 6) in winter than in summer, and there is a tendency for the number of productive trips per day's fishing to be greater in summer. Differences in the number of productive trips per day's fishing are also apparent between years, as in 1953 there were generally more productive trips per day's fishing than in 1952.

To summarize the performances of the two boats, it appears that the ratio of productive trips to the number of day's fishing is greater during times of good fishing and smaller during times of poor fishing. Since trips are shorter when the fishing is good and there are also fewer nonproductive trips, the actual effort in terms of day's fishing will usually be underestimated during the periods of poor fishing as compared with periods of good fishing.

Variations from the official number of crew will also affect the accuracy of the estimate of fishing effort. The official number is a maximum and variations will usually mean that fewer than the official number are aboard. In the Hawaiian skipjack fleet, boats ordinarily carry the maximum number of crew during the summer season, after which some men leave to find other employment. In this study, since the official (maximum) number of crew has been used throughout the year as a weight for the individual trip, the "fisherman" factor in the productive fisherman-trip is probably overestimated during the times of poor fishing.

Thus, the biases in the productive fisherman-trip between times of good and poor fishing tend to cancel each other because during the winter season and years of generally poor fishing, longer trips and the increased frequency of nonproductive trips cause an underestimation of the actual time spent fishing while, at the same time, the actual number of fishermen on the boat is likely to be fewer than the official number. The converse will hold true during the summer season and in years when good fishing attracts the maximum number of fishermen to the fleet.

Information is not available to permit the examination of the actual variations in the number of fishermen and the extent to which they offset the bias introduced by nonproductive trips, but if boat *A* is assumed to represent the average situation, the number of productive trips per day's fishing (col. 11) appears to be about 10 percent greater in summer than in winter. Since the crew of the average skipjack boat is about 10 men, the absence of one of these men on the average during the winter season represents a 10-percent overestimation of the number of fishermen. Thus, the absence of one fisherman per boat during the winter season would be sufficient to equalize the bias in the productive trip factor introduced during the winter season.

SOURCES OF ERROR

Unreported catches or forms containing incomplete or inaccurate information are an obvious source of error. Yamashita (1958, p. 258) estimates that the reported portion of the 1952 catch included 94 percent of the pounds, but only 88 percent of the trips, indicating a bias in favor of the reporting of large catches. Since small catches are most likely to occur in the slack part of the year, there may be a tendency for an estimate of the fishing effort, which is a function of the number of trips, to be correspondingly reduced.

Inaccurate information is difficult to detect without data from other sources with which to compare the catch records. On the basis of interview records, Yamashita (1958, p. 258) estimates that only 45 percent of the statistical areas indicated in the 1952 catch reports were reasonably accurate. By means of broad geographical divisions to summarize the data (fig. 4), it is assumed that the effects of such erroneous information will be minimized.

ERROR IN DETERMINATION OF FISH SIZE

Dividing the total weight caught by the estimated number as indicated in the catch report, yields the average size of fish caught, but provides no indication of the range or variability of sizes. Since the entire catch is assigned to either the small or large category on the basis of the average weight per fish, a certain amount of error will result from mixed catches of small and large fish: this error should distribute itself more or less randomly, however, so that neither size group is consistently favored.

ERROR IN ESTIMATION OF FISHING EFFORT

There is no way to determine from the catch records the actual effort, i.e., the fisherman-days whether productive or not, put forth on a skipjack boat. In this study only positive fishing results (catch reports) are available, and the productive fisherman-trip is of necessity used in lieu of the fisherman-day. Sources of error in the productive fisherman-trip have been discussed in the section, Choice of the Unit of Fishing Effort, and on the basis of the performance of two skipjack boats for which logbooks are available, it appears to be a reasonable substitute.

OTHER SOURCES OF ERROR

The weight of the catch of skipjack taken in the Hawaiian live-bait fishery is affected by complex factors which present sources of error that are difficult to estimate. Among these factors are variations in bait supply, response of skipjack to chum, behavior and number of birds in the flocks which serve to locate schools, the size and behavior of the skipjack schools, selection by the fishermen, and probably several others.

Yamashita (1958, p. 270) has discussed the problem of ascertaining the influence of variations in bait supply on the skipjack catch in terms of annual production and suggests that in certain years, when skipjack have been plentiful, the availability of bait may be a limiting factor in the fishery. Royce and Otsu (1955) have investigated many aspects of behavior of skipjack schools and birds; Yuen (1959) has studied the response of skipjack to live bait.

In the present study no attempt has been made to evaluate the sources of error introduced by the factors considered above. Information available is not adequate to discern which of these may be important at any particular time. It seems reasonable that most of these factors act relatively independent of one another so that over a period of time their combined effects should not introduce bias. However, it is just as plausible that at certain times several of these elements may act in unison resulting in considerable deviation from the normal state. The investigation of the role of these factors in the fishery awaits a more sophisticated study than is attempted here or is possible with the present sources of information.

CONCLUSIONS ON SOURCES OF ERROR

None of the sources of error appears to be so extensive as to destroy the usefulness of the catch report as the basis for a study of distribution and abundance. Some of the sources of error tend to reduce the bias introduced by others. With respect to time, geography, and size, the categories employed in this study have deliberately been made broad. Were the study concerned with only a few vessels, very short time periods, or several size groups, the probability of error would be increased, but as only the most general of categories are used, the influence of error on the results should be slight.

RESULTS AND DISCUSSION

There are small discrepancies between the official total catches for 1952 and 1953 as listed by Yamashita (1958, table 2) and the totals obtained in the present study (table 3). These differences amount to 1 percent and are probably the result of catch reports, which were turned in too late to be included in official summaries and to records lost or misplaced during the interval of storage. The proportion of unusable data in 1953 was greater than in 1952 (table 4), largely because of the poor

TABLE 3.—*Comparative data from 2 studies of the Hawaiian skipjack catch for 1952 and 1953*

Year	Pounds skipjack caught		Difference	Percent difference
	Yamashita [1]	Shippen [2]		
1952	7, 291, 851	7, 390, 882	99, 031	1. 3
1953	12, 059, 406	11, 928, 965	−130, 441	−1. 1

[1] Source: Yamashita (1958, table 2).
[2] Figures adjusted to correspond with calendar year.

TABLE 4.—*Usability of 1952 and 1953 catch report data*

	1952		1953	
	Pounds	Percent	Pounds	Percent
Usable	7, 270, 990	98. 6	11, 345, 013	95. 0
Unusable	105, 453	1. 4	598, 391	5. 0
Total	7, 376, 443	100. 0	11, 943, 404	100. 0

reports from the master of one sampan who consistently summarized his catches by weeks throughout much of the year.

GEOGRAPHICAL DISTRIBUTION OF 1952 AND 1953 CATCHES

Despite the large differences in total landings in 1952 and 1953, the geographical distribution of catch and effort (table 5, fig. 5) is much the same. In both years the leeward Oahu and Hawaii regions furnished approximately 50 and 16 percent of the total catch, respectively, and the oceanic region and Maui were relatively unimportant with less than 8 percent in the aggregate. The combined windward Oahu and Kauai regions contributed about 25 percent of the total catch in each year, but in 1953 a much larger proportion of this came from windward Oahu.

Within the vicinity of Oahu, the distribution of effort appears to be related to the distance from the home port; the amount of effort expended in the zones decreases as their distance from Honolulu increases. This is probably because of the fragile nature of the nehu (*Stolephorus purpureus*), the most important bait species.

CATCH PER UNIT OF EFFORT IN THE HAWAII SKIPJACK FISHERY

If the regions of the fishery from Hawaii in the southeast to Kauai in the northwest are arranged in sequential order (fig. 6), there is some suggestion of an increasing catch per unit-of-effort in the direction of Kauai, but the inequities in the distribution of effort and certain known differences in the local fisheries make it doubtful that the apparent trend is of biological significance. The Hilo (Hawaii) fishermen usually make short trips and land each day's catch on the day it was made,

TABLE 5.—*Geographical distribution of the 1952 and 1953 usable catch data*

[See fig. 4 for location of zones; C/E=catch/effort]

Regions and zones	1952					1953				
	Catch		Effort		C/E	Catch		Effort		C/E
	Pounds	Percent	Units	Percent		Pounds	Percent	Units	Percent	
Oceanic:										
1L	183, 729	2. 5	244	1. 2	753	274, 358	2. 4	439	1. 7	625
1W	128, 458	1. 8	348	1. 8	369	191, 531	1. 7	236	0. 9	812
Total	312, 187	4. 3	592	3. 0	527	465, 889	4. 1	675	2. 6	690
Hawaii:										
3L	252, 659	3. 5	1, 073	5. 4	235	485, 317	4. 3	1, 572	6. 2	309
3W	881, 673	12. 1	2, 869	14. 6	307	1, 288, 967	11. 4	3, 676	14. 4	351
Total	1, 134, 332	15. 6	3, 942	20. 0	288	1, 774, 284	15. 6	5, 248	20. 6	338
Maui:										
4L	115, 113	1. 6	119	0. 6	967	25, 257	0. 2	62	0. 2	407
4W	139, 939	1. 9	463	2. 4	302	179, 291	1. 6	452	1. 8	397
Total	255, 052	3. 5	582	3. 0	438	204, 548	1. 8	514	2. 0	398
Inshore Oahu:*										
5L	2, 259, 734	31. 1	7, 350	37. 3	307	3, 365, 538	29. 7	9, 116	35. 7	369
5W	719, 780	9. 9	1, 952	9. 9	369	1, 742, 242	15. 3	3, 266	12. 8	534
Total	2, 979, 514	41. 0	9, 302	47. 2	320	5, 107, 780	45. 0	12, 382	48. 5	413
Offshore Oahu:*										
2L	1, 486, 181	20. 4	3, 519	17. 9	422	2, 656, 150	23. 4	5, 022	19. 7	529
2W	157, 854	2. 2	361	1. 8	437	415, 346	3. 7	674	2. 6	616
Total	1, 644, 035	22. 6	3, 880	19. 7	424	3, 071, 496	27. 1	5, 696	22. 3	539
Oahu region subtotals:*										
L	3, 745, 915	51. 5	10, 869	55. 2	345	6, 077, 707	53. 6	14, 242	55. 8	427
W	877, 634	12. 1	2, 313	11. 7	379	2, 212, 112	19. 5	3, 990	15. 6	554
Region total	4, 623, 549	63. 6	13, 182	66. 9	351	8, 289, 819	73. 1	18, 232	71. 5	455
Kauai:										
6L	284, 845	3. 9	560	2. 8	509	217, 722	1. 9	373	1. 5	584
6W	661, 025	9. 1	844	4. 3	783	392, 751	3. 5	462	1. 8	850
Total	945, 870	13. 0	1, 404	7. 1	674	610, 473	5. 4	835	3. 3	731
Grand total	7, 270, 990	100. 0	19, 702	100. 0	369	11, 345, 013	100. 0	25, 504	100. 0	445

*The Oahu region includes inshore and offshore Oahu, 2L, 5L, 2W, and 5W. For 1953, a few additional catches were made across zone boundaries within the Oahu region.

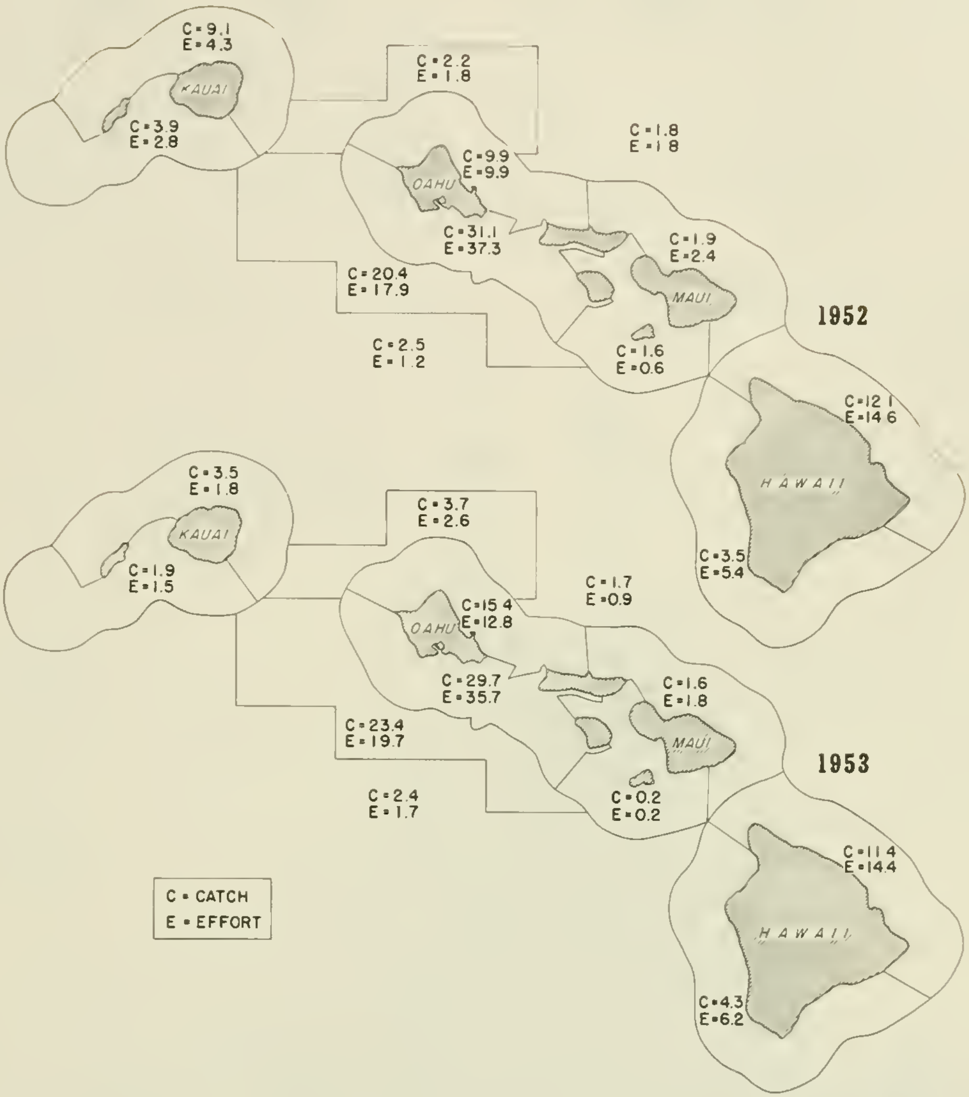


FIGURE 5.—Geographical distribution of catch and effort in the Hawaiian skipjack fishery, 1952 and 1953.

whereas the trips by Honolulu-based fishermen to the vicinity of Kauai are longer than a single day; therefore, the differences in time-of-trip between the two areas are probably significant.

Similarly, catch per unit of effort tends to increase with increasing distance from shore (fig. 7). Only a fraction of the total effort was expended in the oceanic region as compared with the effort inshore, and a few good catches of large fish may have produced an index far out of proportion to the actual apparent abundance. Royce and Otsu (1955, p. 18), however, report sighting more tuna schools per day's scouting beyond 19 miles from shore than were seen within 19 miles of shore.

SIZE OF SKIPJACK AND POUNDS CAUGHT PER UNIT OF EFFORT

There is a positive correlation (fig. 8) between the average size of skipjack caught in zones of the fishery during the year (table 6) and corresponding catch per unit of effort (table 5). Zones with less than 5 percent of the total annual effort are not included in the analysis because they are unlikely to represent fishing conditions throughout the year. This correlation appears to substantiate the observation that the larger skipjack usually can be caught more efficiently than the smaller, up to the size at which individuals must be gaffed in landing and the efficiency drops.

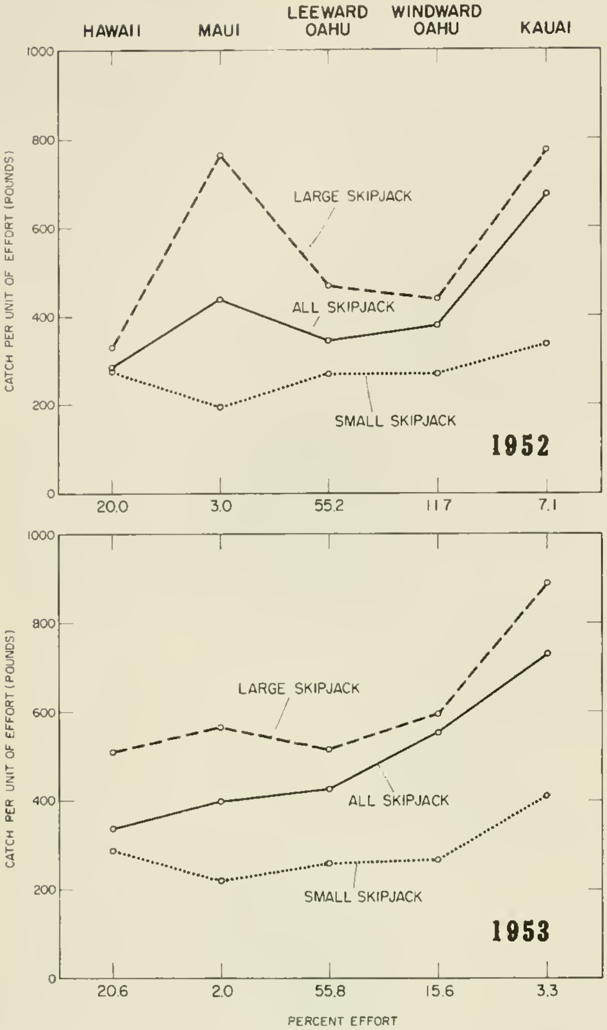


FIGURE 6.—Pounds caught per unit of effort by island regions.

TABLE 6.—*Average weight of skipjack caught in each zone of the fishery*

Zone	1952	1953	Zone	1952	1953
	Average weight (pounds)	Average weight (pounds)		Average weight (pounds)	Average weight (pounds)
1L	15.5	18.2	4L	14.5	12.1
1W	7.9	14.7	4W	11.9	13.0
2L	*9.0	*13.9	5L	*8.2	*11.2
2W	17.2	15.9	5W	*9.2	*12.8
3L	*4.8	*7.7	6L	6.7	11.5
3W	*4.8	*7.5	6W	12.8	8.1

*Indicates zones receiving more than 5 percent of the total fishing effort during the year.

Each year the small fish are caught in Hawaii (zones 3L and 3W); the larger fish are from inshore windward Oahu (5W), and offshore leeward Oahu (2L). The association of small fish with

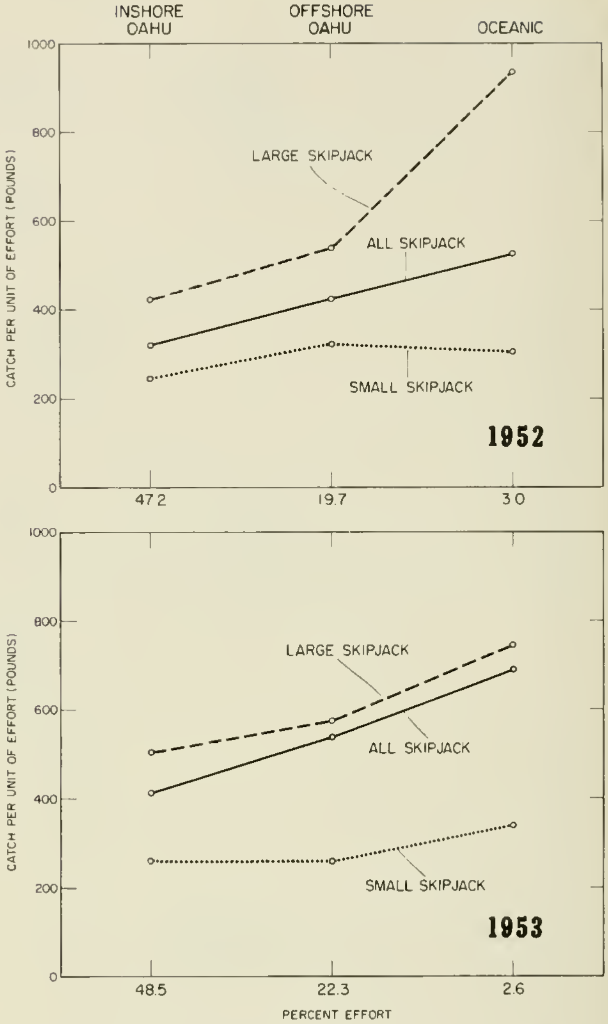


FIGURE 7.—Pounds caught per unit of effort by distance from shore.

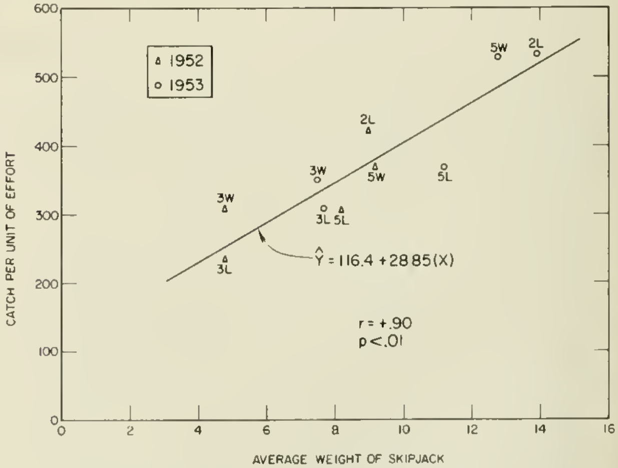


FIGURE 8.—Regression of catch per unit of effort on average weight of fish caught.

Hawaii may be explained by the nature of the fishery there, which is based largely on semiresident populations of small skipjack. Other populations of small fish are known to occur in inshore areas of leeward Oahu (5L), and these are usually exploited when the large skipjack are in low abundance and produce the intermediate average weight for zone 5L. Zones 5W and 2L are more remote from Honolulu than is 5L, and it seems probable that the fishery in these zones may be biased in favor of periods when large skipjack are available, which could account for the relatively greater average weight per fish in these zones of the fishery.

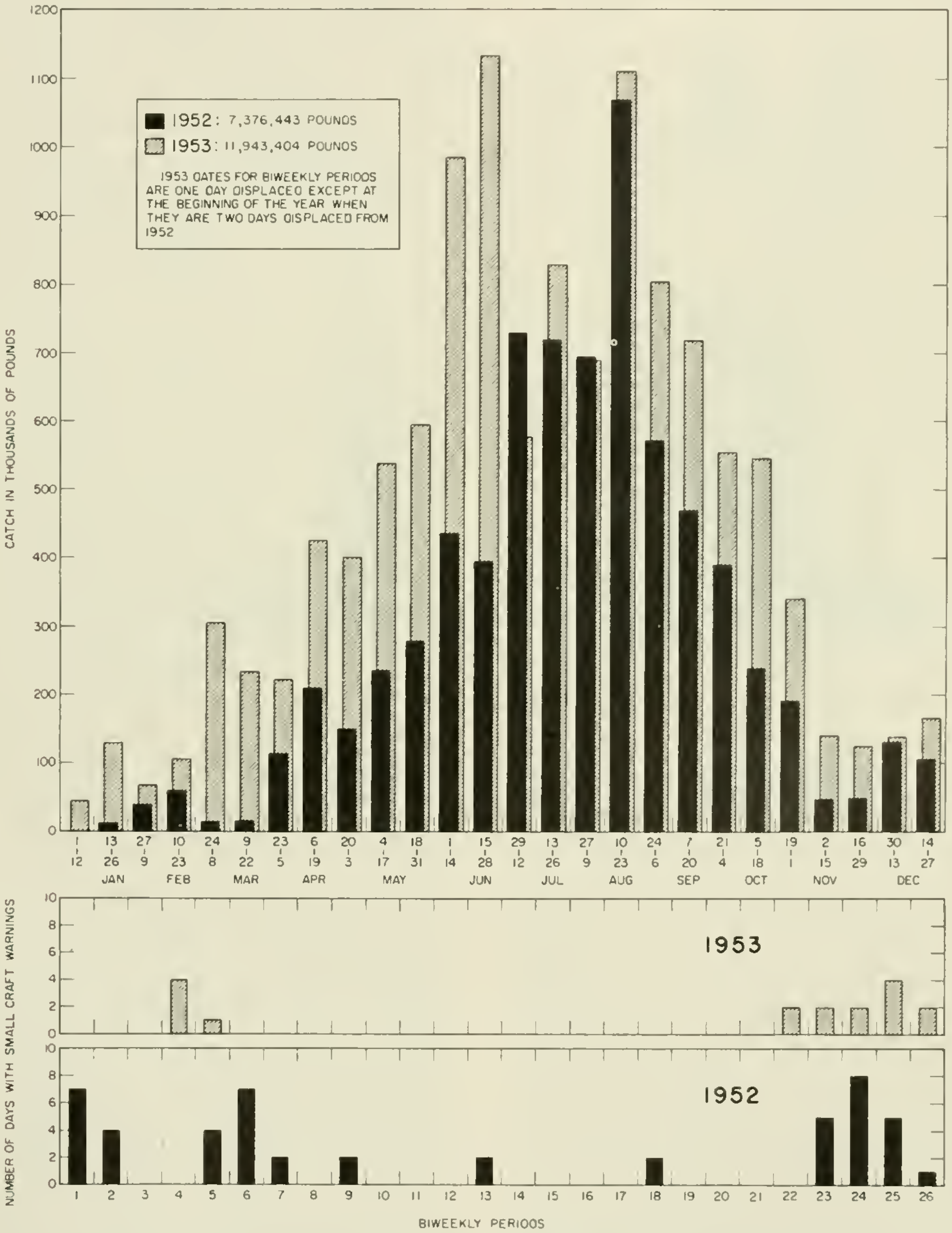


FIGURE 9.—Catches (pounds) of the Hawaii skipjack fishery, 1952–1953, by biweekly periods. Periods of small craft warnings are shown below.

DISTRIBUTION OF 1952 AND 1953 CATCHES BY BIWEEKLY PERIODS

Catches for the Entire Fishery

Only during July and August (periods 14–17) and briefly in December (period 25) did the 1952 skipjack catches reach the magnitude of the 1953 totals (fig. 9). In particular, the spring of 1953 and, to a lesser extent, the autumn months provided much larger catches than occurred in 1952.

Effects of Small Craft Warnings

There were 49 days with small craft warnings during 1952 and 17 during 1953 (fig. 9), but only 6 of these fell in the interval from April through September in 1952 and none in 1953. The effects of rough weather, therefore, appear to be relatively minor in comparison with the seasonal fluctuation in the availability of skipjack.

The immediate effects of poor weather may be indicated by the relatively small catches made during periods 1, 2, 5, 6, 23, and 24 of 1952, each of which had several days with small craft warnings. Period 25, on the other hand, shows an increase in catch despite 5 days of poor weather.

MOVEMENTS OF SKIPJACK WITHIN THE FISHERY

Local changes in the skipjack catch within the entire range of the fishery may result from changes in the amount of fishing effort or from changes in availability. The latter may include horizontal movement of the fish into or out of a particular area or, within an area, a change in the vertical distribution or behavior such that the catch rate by live bait fishing is affected. The records of the fishery, however, provide no means by which one or the other cause may be determined, and it is therefore assumed for the purposes of this discussion that all changes in the catch are caused by movements of fish from one area to another. Thus, errors, if any, are likely to be on the side of postulating a horizontal movement of fish when there has been a change in vertical distribution, behavior, or fishing effort. This approach seems to be the most reasonable one, because tagging experiments show that individual skipjack travel the length and breadth of the fishery, while knowledge of changes in availability and fishing effort, particularly if nonproductive, remains quite limited.

Large Skipjack

After an interval of low abundance throughout the islands during the early part of 1952, large skipjack (fig. 10) appeared simultaneously in small numbers in leeward Oahu and Kauai in period 8. In period 10 the fish arrived in windward Oahu and Hawaii. This sequence suggests an approach from the west. In period 12, a concentration centered in windward Oahu occurred; it appears to have shifted northward to Kauai by periods 15 and 16. In period 17, however, the catches of large skipjack ceased in Hawaii and began to dwindle in Kauai, but at the same time the largest catches of the year were being made in leeward Oahu. All these changes seem to indicate that the large skipjack had returned to the leeward side of the island chain. The gradually diminishing catches from Kauai and leeward Oahu in periods 18 through 20 indicated the withdrawal of season fish to the westward. After period 20, the numbers of large skipjack in the catch returned to the state of low variable abundance which characterizes the off-season of the fishery.

During the interval from period 25 (1952) until period 4 (1953) the number of large skipjack taken in all regions of the fishery was uniformly low, a condition typical of the winter season. In period 5, however, a sharp increase occurred in the catch of large skipjack in the leeward Oahu region. To judge from the variation in average weights (fig. 12), these fish were 1952-season fish, being somewhat heavier than 1953-season fish which entered the fishery in period 9. These 1952-season fish appeared in the catches during periods 5, 7, 8, and 9 and were the cause of the apparent early beginning of the "season" in 1953 (fig. 9).

In period 9 of 1953, the season fish were present throughout most of the fishery (note the declining average weights in periods 9 and 10, fig. 12) but the large catches in leeward Oahu in periods 10 through 12 suggest that the direction of the approach of the main body of fish was from the leeward. As in the previous year, a peak occurred early in the season in windward Oahu (period 12, 1952; period 13, 1953), and in succeeding periods the fish dispersed southward to leeward Oahu and Hawaii where large catches were made in periods 15–17. Following the excellent catches of period 17, the best of the year, a gradual decrease in catch occurred, and by period 23 the season was over.

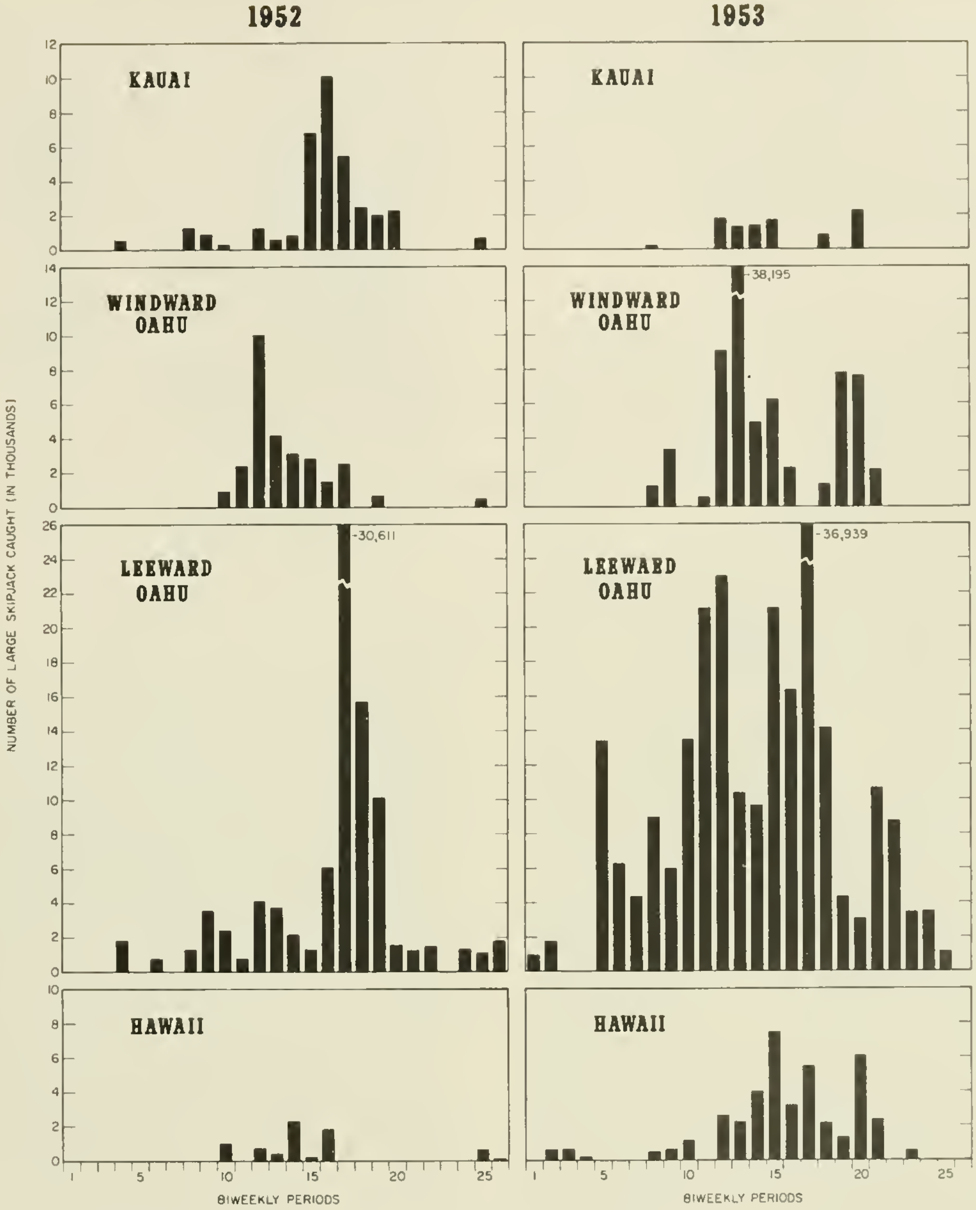


FIGURE 10.—Number of large skipjack caught (1952–53); biweekly periods.

Certain features common to both years are to be noted: (1) the approach of the large fish at the start of the season, apparently from the leeward; (2) the concentrations on the windward and leeward sides of Oahu in June and August, respectively; and (3) the final disappearance of fish to the leeward. Differences in the 2 years are as follows: (1) the appearance in the early part of 1953 (period 5) of large skipjack, and (2) the direction of movement of the season fish between the time of the windward Oahu peak catches (periods 12–13) and the leeward Oahu peak (period 17). In 1952 the fish went northward to Kauai and thus close to the limit of the fishery. In 1953 they returned to leeward Oahu and Hawaii to remain well within the range of the Honolulu and Hilo based vessels.

In general, the movements of large skipjack, as indicated by their occurrence in the commercial catch, do not suggest an orderly migration along the island chain. The reason for this may be in the direction of approach of the migrating schools, which appears to be perpendicular rather than parallel to the barrier formed by the islands. The relative speed with which schools travel, which may reach 15 knots (Royce and Otsu, p. 18), may be such that a period of 2 weeks is too long to discern a migratory pattern within an area as small as that encompassed by the Hawaiian skipjack fishery.

Small Skipjack

Examination of the numbers of small skipjack caught and the corresponding catch per unit-of-effort data revealed no discernible pattern of movement within the fishery. Large skipjack are the prime objective of the fishery and the smaller sizes are usually taken as a second choice. The number of small skipjack in the catch, therefore, tends to be a function of the number of large fish available. The relationships between the numbers of large and small fish in the catch are discussed under the section, Size Composition.

OAHU SKIPJACK FISHERY, 1952 AND 1953

STATISTICAL COMPARISONS

The comparative statistics for 1952 and 1953 in the Oahu region are summarized in table 7. In almost every way, 1953 reflects the greater availability of skipjack than in the previous year, as evidenced by (1) a much larger catch, (2) almost half as much fishing effort, and (3) a larger catch per unit of effort. The number of small skipjack caught (4b) and pounds caught per unit of effort (3b) are not markedly different between years, but the catch of large fish, both in absolute numbers (4a) and on a relative basis (3a), is considerably greater in 1953. Most of the differences between the 2 years can be attributed to the abundance of this size group in the fishery.

Independently of size considerations, the number of fish taken per biweekly period in 1953 was larger than the corresponding number in 1952 (5 and 6). The relative abundance of large and small skipjack in the 2 years is indicated by the number caught per unit of effort (7) which is greater for the small fish in 1952 and for the large fish in 1953. The importance of the abundance of large fish to the success of the fishery may be measured by the comparative number of biweekly periods in the various categories (8).

TABLE 7.—*Comparative statistics for the Oahu fishery, 1952 and 1953*

	1952	1953	1953/1952
1. Total pounds caught	4, 623, 549	8, 715, 958	1. 89
(Percent of total for skipjack fishery)	(63)	(73)	----------
a. Large skipjack only	2, 058, 921	6, 366, 336	3. 09
b. Small skipjack only	2, 564, 628	2, 349, 622	. 92
2. Total productive effort	13, 182	19, 169	1. 45
a. Large skipjack, percent	34	55	----------
b. Small skipjack, percent	66	45	----------
3. Pounds caught per unit of effort, all usable catches	351	455	1. 30
a. Large skipjack only	462	533	1. 15
b. Small skipjack only	270	261	. 97
4. Total number of fish caught	521, 500	677, 000	1. 30
a. Large skipjack only	123, 500	330, 500	2. 67
b. Small skipjack only	398, 000	346, 500	. 87
5. Average number caught per biweekly period	20, 577	26, 038	1. 27
6. Median number of skipjack caught in each year for the 26 biweekly periods	18, 044	25, 833	1. 43
7. Number of fish caught per unit of effort	40	35	. 88
a. Large skipjack only	28	31	1. 11
b. Small skipjack only	46	40	. 87
8. Number of biweekly periods with—			
a. more than 300,000 pounds catch	5	14	2. 80
b. more than 800 units fishing effort	5	11	2. 20
c. more than 400 pounds catch per unit of effort	5	14	2. 80

RELATIONSHIPS BETWEEN CATCH STATISTICS

The population indices derived from the catch reports are the raw catch and the relative catch; i.e., catch per unit of effort. Either index may be in terms of weight or number of fish and may be calculated for the entire catch or for limited categories. Since 1954, however, no information on the number or size of fish in the catch has been included in the catch report, so the only indices which may be considered for recent years in the fishery are the pounds caught and the catch per unit of effort without respect to size categories.

The biweekly statistics for pounds caught, catch per unit of effort, and effort within the Oahu region for 1952 and 1953 are plotted in figure 11. Of particular interest here is the relation between the raw catch and the catch per unit of effort, for if the two show essentially the same variation, there is little or no advantage to be gained in employing catch per unit of effort as the index of apparent abundance.

It is obvious from figure 11 that there is much similarity in the fluctuations of all three indices; each has a seasonal variation on which lesser fluctuations are superimposed. Additionally, there is a secular trend from 1952 to 1953. The catch curve tends to change gradually and peak sharply, while the effort curve changes rapidly at the start and close of the season, with little trend during midyear.

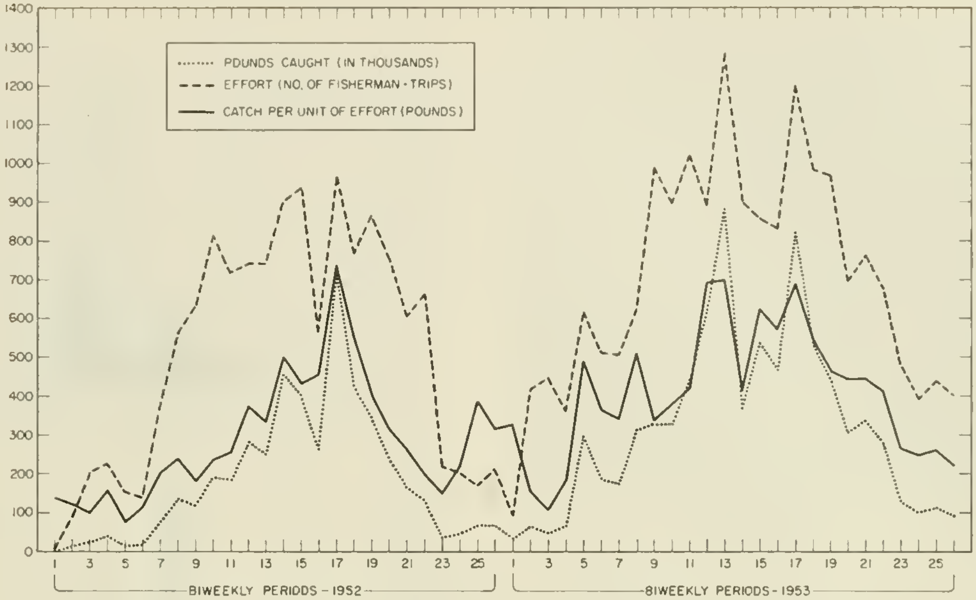


FIGURE 11.—Oahu region catch statistics, 1952 and 1953, biweekly periods.

The results of these tendencies in catch and effort curves on the catch per unit-of-effort curve are as follows: (1) During midyear when effort tends to be constant, the catch per unit of effort will closely follow the fluctuations in catch. (2) During the onset and decline of the season, effort is changing more rapidly than catch and the catch per unit of effort will change at an intermediate rate. Random fluctuations in the catch per unit-of-effort at this time may be somewhat at variance with those in the catch, as occurred in the interval from period 24, 1952, to period 3, 1953.

Correlation analysis between raw catch and catch per unit-of-effort data yields a coefficient of +0.92. It was necessary to use rank correlation methods (Snedecor, 1956, p. 190) because the distribution of catches is skewed toward small catches. In order to determine the amount of agreement between the random fluctuations in the two indices, the first differences were correlated and yielded a coefficient of +0.79. Conventional methods were used here because the first differences are distributed more normally than the original series. The probability that correlation coefficients this large would occur by chance is less than 0.01.

The variate-difference technique (Kendall, vol. II, p. 387–390) was used to obtain an estimate of the variance in the random component of each index compared to the variance of the original series. The values obtained for the random components were 24 percent for the raw-catch series and 18 percent for the catch per unit-of-effort series. Since it exhibits a smaller random component, the catch per unit-of-effort series appears to be somewhat more reliable than the catch as an index of skipjack availability, but only slightly so.

In summary, the raw catch is almost as accurate as the catch per unit of effort in indicating the seasonal variation in skipjack abundance in the Hawaiian fishery. During the middle of the year the raw catch is in good agreement with the random fluctuations in catch per unit of effort, but during the off-season of the fishery, when effort and catch are either declining rapidly or are at a low level, random fluctuations in catch per unit of effort may not vary in agreement with fluctuations in catch. For most purposes, total catch would appear to be as useful an indicator of availability as the catch per unit of effort, especially in problems where the seasonal trend in the fishery is apparent.

USE OF CATCH RECORDS TO DETERMINE POPULATION COMPOSITION

The catch statistics of the Hawaiian fishery are the only continuous source of information which provides a means of assessing the nature of the skipjack population which supports the fishery. Inferences about this population must be made with caution, however, because the fishery is limited geographically to the immediate island area (fig. 4). Furthermore, the catches are also influenced by availability, fishing effort, and selectivity on the part of the fishermen, which may not be constant throughout the year. Brock (1954, p. 100–103) has shown, by means of sex ratios, that the availability of female skipjack is not constant. He suggests that spawning activity may be the crucial element. The cyclical nature of fishing effort has been shown previously (fig. 11), and the fact that the fishermen are selective in the schools they fish is common knowledge. These biases appear to have an annual cycle and between-year comparisons may not be affected by them to the extent of within-year comparisons.

Fluctuations in the Catch of Large Skipjack in the Oahu Region

The growth rate of Hawaiian skipjack has been studied by Brock (1954, pp. 96–97) by means of length frequency distributions. During the summer there are two distinct modes, one at about 45 cm. (4 pounds) and one at about 70 cm. (18 pounds).[1] The mode of large skipjack represents season-fish and presumably a smaller number of the previous year's season-fish. It is this mode that is considered here as large skipjack. The time of year when a mode, which Brock assumes to be a year class, passes through the weight (10 pounds) which separates small and large fish in this study, is apparently winter or early spring. During the period from May to October, it may be assumed with reasonable certainty that the small skipjack are a year younger than the large skipjack.

In 1952 there appears to be little consistency in the average weight for large skipjack (fig. 12), which fluctuates widely from one biweekly period to the next. By contrast, 1953 has an interval from May 3 through October 3 (periods 10–20) with a regularly increasing weight for large fish. The rate of this increase, 0.25 pound per week, is in agreement with Brock's curve for skipjack growth, which yields a linear weight increase of 0.25 pound per week. The coincidence of the season of greatest productivity (as indicated by the number of large fish caught) with the interval of uniform weight increase suggests that in 1953 a single population of season skipjack was available to the fishery, but the erratic fluctuation in the numbers taken indicates that variations in this availability were quite marked.

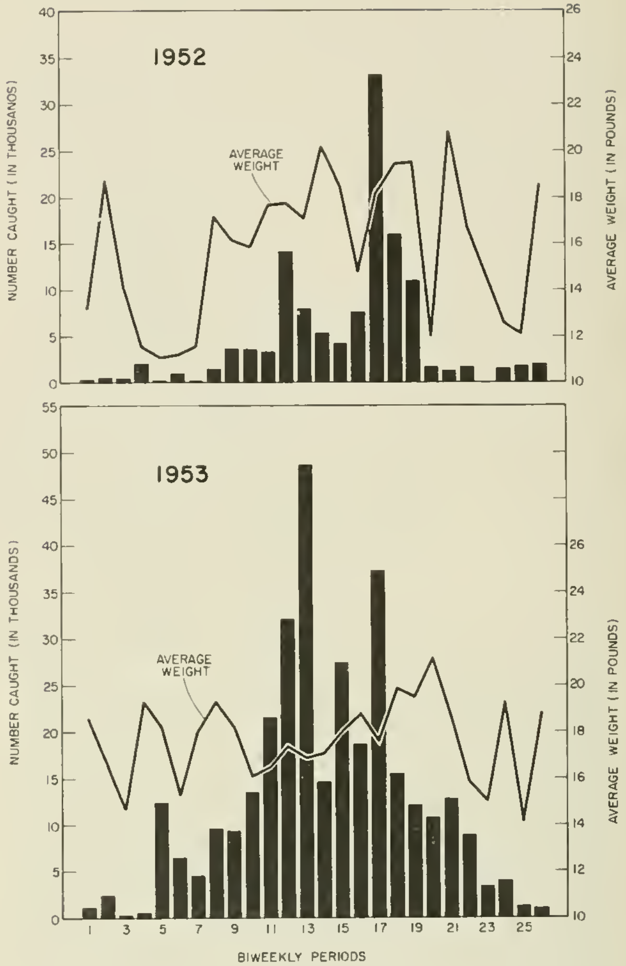


Figure 12.—Catch of large skipjack in the Oahu region, 1952 and 1953.

Period 5 of 1953, with its unusual numbers of very large fish, must consist of skipjack greater in size than the 1953-season fish. It seems probable that these very large skipjack are 1952-season fish, which were present only briefly that year. The relatively high average weights during other periods of early 1953 imply that 1952-season fish may have been generally present during that time. In early 1952, on the other hand, few of the previous year's season fish were present, as judged by the average weights during periods 4 to 7.

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[1] Conversions of length (millimeters) to weigh (pounds) were made according to the formula: Log weight$= -8.2755+3.34913$ log total length.

Size Composition

Small skipjack are usually sought by the fishermen only when they are unable to locate larger fish. One would expect, therefore, that the occurrence of small fish in the catch would be inversely related to the presence of the larger skipjack, and this does seem to be the situation. The numbers of large and small skipjack taken in the Oahu fishery in each biweekly period of the 2 years under study is plotted in figure 13. In 28 biweekly periods (1952, 8–20; 1953, 8–22) when large skipjack were generally present, a tabulation was made to see how frequently the changes in the number of one size group were associated with similar or opposite changes in the other. Opposite trends, e.g., the number of large skipjack decreases from the preceding period while the number of small skipjack increases, occur in 22 periods while similar trends occur in 6. The probability of obtaining such a distribution if the numbers of large and small fish in the catch fluctuate independently of one another is less than 0.01.

Size composition appears to be important in the determination of the general level of catch (fig. 14) and the pounds caught per unit-of-effort (fig. 15). Both increase rapidly with an increasing proportion of large fish up to a ratio of 1 large fish for 1 small fish. Above this ratio the total catch continues to increase at a fairly rapid rate, but catch per unit of effort increases at a slower rate.

The likelihood of catches of large numbers of individuals seems to be loosely linked with the size composition. During the interval included in this study, the largest numbers of skipjack were taken either when small fish were especially numerous and very few large fish were available or when large skipjack were in a majority (fig. 16). When small fish outnumber the large, but are less than 10 times as numerous, there seem to be factors that work against the capture of a large number of individuals. These factors, if they exist, are probably related to the distribution of the various size groups in the population which supports the fishery. A hypothesis concerning the structure of this population is offered below.

Conjecture

In order to account for the variations in apparent abundance of particular size groups in the catches, it is necessary to hypothesize a skipjack population consisting of at least three and possibly one additional element. In the approximate order of their importance to the success of the fishery in 1952–53, these are as follows:

Group A: "Season fish," approximately 17–22 pounds in weight, which Brock assumes to be in either their second or third year of life. This group is migratory.

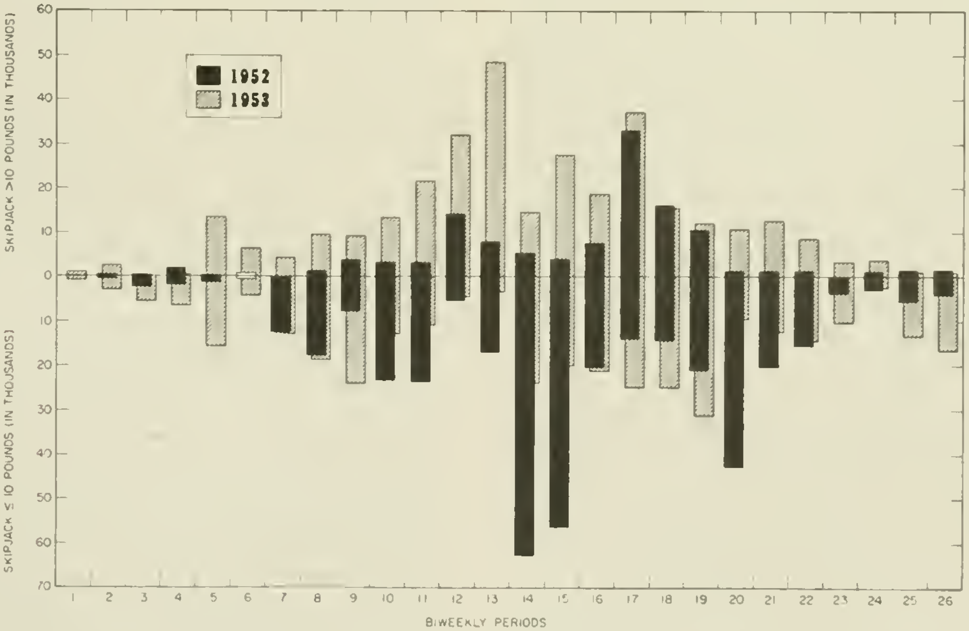

FIGURE 13.—Estimated numbers of large and small skipjack taken in the Oahu fishery, 1952–53, by biweekly periods.

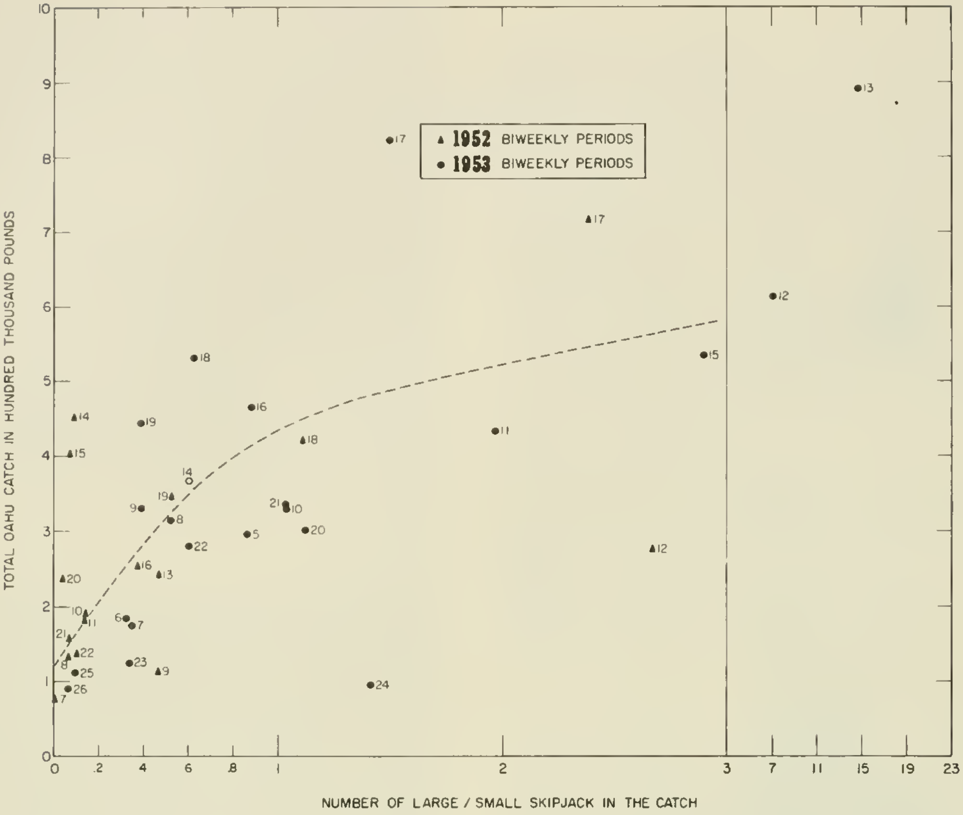

FIGURE 14.—Size composition and the total catch in the Oahu skipjack fishery, 1952–53.

Group B: Nonmigratory small fish, which during the summer months are about 4 to 8 pounds in weight. These fish occur in semi-permanent aggregations which are to be found in certain localities, usually near shore, where presumably oceanographic conditions are suitable for the concentration of food organisms. These fish, according to Brock's hypothesis, are a year younger than the season fish. This group serves as the main source of supply for some of the fishermen, but in general it functions as a reserve supply where most of the fishermen can use their bait, when larger fish are not available.

Group C: Large migratory skipjack, 28–32 pounds, which may be a year older than the season fish. This group seems to have been abundant during the first part of 1953 and accounts for the apparent early begining of the season in that year.

Group D: Migratory small skipjack. The existence of this group is not well established; however, the large numbers of small fish which appear suddenly in the fishery in periods 14, 15, and 20 of 1952 suggests that there may be a migratory group of small fish as well as the semiresident group.

In figure 16, catches of large skipjack numbering in excess of 15,000 were all made when season fish (group A) were apparently dominant in the fishery; the large catches of small skipjack, those in excess of 40,000, are presumed to result from the presence of migratory small fish (group D). The sharp decline in the number of periods with catches of small skipjack greater than 25,000 may indicate that this number is about the maximum number of nonmigratory fish (group B), which are available during a biweekly period. Except for period 17, 1953, the number of small fish in the catch declines as the number of large fish increases, which is consistent with the assumption that the number of small fish caught is inversely related to the availability of large fish. The extra-large migratory fish (group C) are distinguished by their greater average weight relative to the season fish, and not, at least during 1952–53, by their unusually large numbers. At the time of

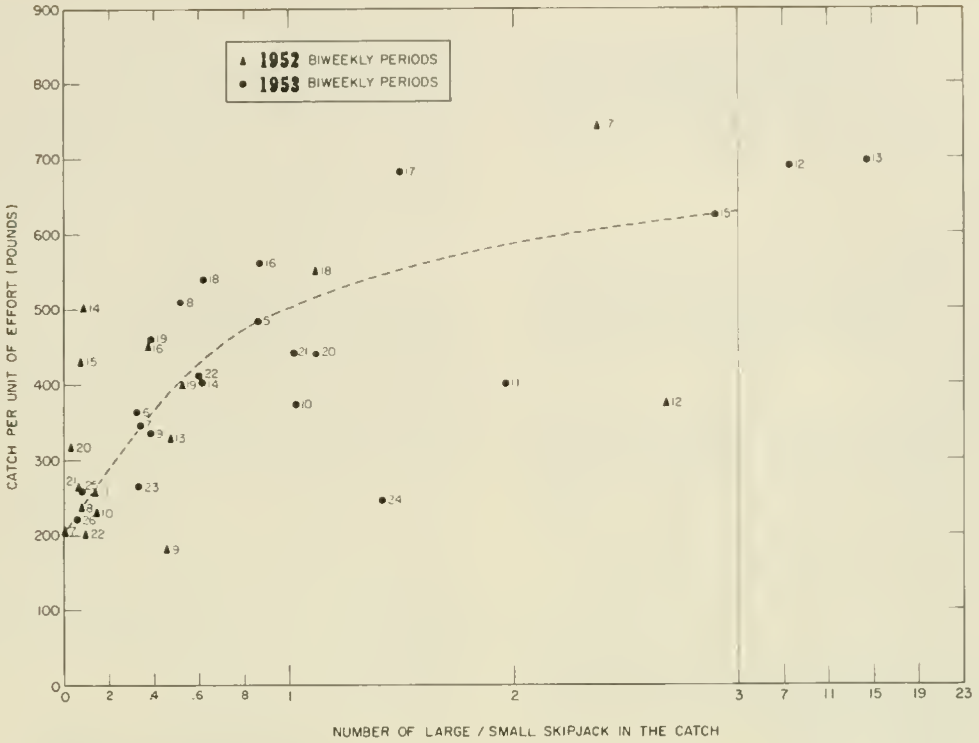

Figure 15.—Size composition and catch per unit-of-effort in the Oahu skipjack fishery, 1952–53.

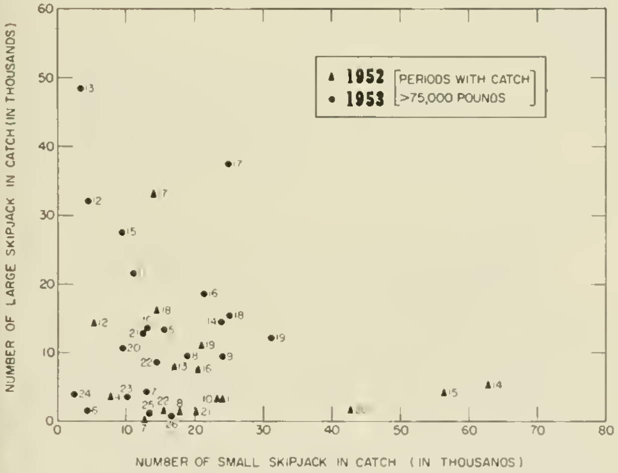

Figure 16.—Size composition and the number of skipjack caught in the Oahu fishery, 1952–53.

their appearance in the catch during periods 5 and 7–9, 1953 (fig. 12), they were associated with fairly large numbers of the nonmigratory small fish.

The fact that the three migratory groups seem to occur at different times suggests that there is little overlap in their distribution, but the catch records do not show this with certainty, for (see Sources of Error) the average weight of fish in the catch is a none too adequate index of size composition. The actual distribution of small skipjack is not defined by their appearance in the catch. It is possible that during the periods when the catch consists predominantly of large fish, small skipjack are also available, but have been rejected by the fishermen. In order to obtain information as to the quantity of small fish actually present, a method such as maintenance of logbooks in which the fishermen could record their observations of all fish sighted, whether fished or not, would be required.

The catch records provide little means of determining the relations between the four groups of skipjack which seem to make up the population exploited by the Hawaii fishery. It is quite probable that the small fish in both the migratory and semiresident groups furnish recruits for the season fish. The season fish of a given year may be the large fish of the next year. The long-term recovery of tagged specimens would appear to offer the best means of ascertaining the relations between these different groups of fish.

SUMMARY

1. The staff of the Honolulu Biological Laboratory is trying to determine the environmental conditions which influence the local availability of skipjack. Commercial catch records are a source of information.

2. Methods and sources of error are considered. Fish catch reports for 1952 (a poor year) and 1953 (a good year) were summarized by areas of the fishery and biweekly fishing periods. The unit of fishing effort, the productive fisherman-trip, is discussed.

3. The distribution of catches and effort in the 2 years was generally similar, with leeward Oahu contributing one-half the catch. Hawaii, windward Oahu, and Kauai fell well below leeward Oahu in productivity, while Maui and the oceanic region contributed insignificant proprotions.

4. Pounds caught per unit of effort increased from southeast to northwest in the fishery and from inshore to offshore, but these trends may result from differences in the fishery rather than to distribution of fish.

5. There was a positive correlation between the average weight per skipjack caught in various zones of the fishery and catch per unit of effort.

6. Catches (in pounds) during the fishing periods of 1953 were, with few exceptions, larger than those made during the corresponding periods of 1952.

7. In comparison with the seasonal trend in the fishery, the effects of rough weather (as indicated by periods of small craft warnings), were unimportant.

8. Large skipjack, from their appearance in the catches, seemed to have arrived first in leeward areas, and at the end of the season they last appeared in catches from leeward areas. In June and August of both years, concentrations of season fish occurred in windward Oahu and leeward Oahu, respectively.

9. The numbers of small fish taken by the Oahu fishery in 1952 and 1953 were approximately equal, but almost three times as many large fish were caught in 1953. In the Oahu region, there was almost one and one-half times the fishing effort in 1953 in comparison with 1952, and a much larger proportion was directed toward catching large skipjack.

10. Catch, effort and catch per unit of effort indexes have similar seasonal variations. The positive correlation between catch and catch per unit-of-effort is so close that there is little to be gained in using the catch per unit-of-effort as an index of apparent abundance in the fishery.

11. During the middle of 1953, the average weight of large skipjack increased at 0.25 pound per week, the growth rate for Hawaii skipjack estimated by Brock. This suggests that fish of the same age were constantly available to the fishery during this period.

12. The number of small skipjack in the catch varied inversely with the number of large fish.

13. A hypothesis for the structure of the skipjack population supporting the fishery is offered. The population has four groups: (1) season fish and (2) extra-large fish, both of which are migratory, and (3) a semiresident and (4) a migratory group of smaller skipjack.

LITERATURE CITED

Brock, V. E.

1954. Some aspects of the biology of the aku, *Katsuwonus pelamis*, in the Hawaiian Islands. Pacific Science 8(1) : p. 94–104.

June, F. C.

1951. Preliminary fisheries survey of the Hawaiian-Line Islands area. Part III. The live-bait skipjack fishery of the Hawaiian Islands. U.S. Fish and Wildlife Service, Commercial Fisheries Review 13(2) : p. 1–18.

Kendall, M. G.

1951. The advanced theory of statistics. Vol. II. Third edition. Charles Griffin & Co., Ltd., London, England. 521 p.

Royce, W. F., and T. Otsu.

1955. Observation of skipjack schools in Hawaiian waters, 1953. U.S. Fish and Wildlife Service, Special Scientific Report—Fisheries No. 147, 31 p.

Snedecor, G. W.

1956. Statistical methods, 5th edition. The Iowa State College Press, Ames, Iowa. 534 p.

Yamashita, D. T.

1958. Analysis of catch statistics of the Hawaiian skipjack fishery. U.S. Fish and Wildlife Service, Fishery Bulletin 134, vol. 58, p. 253–278.

Yuen, H. S. H.

1959. Variability of skipjack response to live bait. U.S. Fish and Wildlife Service, Fishery Bulletin 160, vol. 60, p. 87–106.

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ABUNDANCE AND AGE OF KVICHAK RIVER RED SALMON SMOLTS

By ORRA E. KERNS, JR.

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ABSTRACT

Standardized methods are described for use of an index fyke net to determine annually the abundance of smolt migrations from the Kvichak River system, Bristol Bay, Alaska. Details of the fyke-net construction are presented. The fyke-netting procedure and the fishing season are discussed as well as some of the more important river conditions for an effective fyke-net site: water velocity and depth, channel changes, and debris. Annual indices of smolt abundance for the years 1955 through 1959 are presented. Comparisons in the timing of migration between years are included. Results of tests to determine the variation between sizes of catch and age composition of fish taken in nets fished side by side and up and down river are described. Information is presented showing that large parent escapements produced large smolt migrations and small escapements produced small smolt migrations.

A sampling program of fyke-net catches to determine age composition is described. Age composition has been based on length-frequency and scale studies. Age composition for each year is presented. Smolt age composition has been compared with fresh-water age composition of returning adults.

ABUNDANCE AND AGE OF KVICHAK RIVER RED SALMON SMOLTS

By Orra E. Kerns, Jr., *Senior Fisheries Biologist*
University of Washington

Two essentials to managing a fishery for red salmon, *Oncorhynchus nerka* (Walbaum), are knowledge of the abundance and of the ages of the smolts as they leave a river system on their way to the sea. When the abundance and ages of the smolts are related for a number of years to the number and ages of the returning adults, predictions can be made of the size of subsequent adult returns. These data are particularly important in the Kvichak River, since it is the largest red salmon producing system in Alaska.

Specific objectives of red salmon smolt studies in the Kvichak River system were (1) an index of the abundance, and (2) the age composition of the entire migration.

Our method of assessing smolt abundance is based on the catch of a single fyke net. Gear and fishing effort expended are kept constant, but the fishing site is changed slightly to provide uniform water depth and velocity. Combined daily fyke-net catches for the season provide an index of total smolt migration (Burgner, 1958).

An index of abundance is not as desirable as an enumeration of the total migration, which has been explained by Foerster (1929), Krogius and Krokhin (1948), and the International Pacific Salmon Fisheries Commission (1955), but a total enumeration in the Kvichak River system has not been practical. Suitable gear has not been developed to cope with the width, depth, and velocity of the river. Therefore, we have located and operated the fyke net in such a manner that we think it reasonable to assume a constant (but unknown) ratio of the fyke-net catch to the total migration.

Samples for the determination of age composition of the smolt migrations were taken from the fyke-net catches. Age composition has been based on smolt length-frequency and scale studies.

The Kvichak River drainage basin covers nearly 8,000 square miles. Included are two major lakes, Iliamna Lake, which is 80 miles long, 20 miles wide, and 1,115 square miles in area; and Lake Clark, which is 50 miles long, 4 miles wide, and 143 square miles in area (fig. 1). Iliamna Lake is about 50 feet above sea level and Lake Clark is about 220 feet above sea level (U.S. Army Corps of Engineers, 1957).

From 1947 through 1954 studies of age composition and sex ratio of the Naknek-Kvichak commercial catch and spawning-ground escapements were conducted annually by staff members of the Fisheries Research Institute, University of Washington. In the spring of 1955, at the request of Alaska Salmon Industry, Inc., systematic observations of red salmon runs in the Kvichak River system were initiated by the Institute under contract with the U.S. Bureau of Commercial Fisheries. Expanded investigations since 1955 were designed to measure mortalities at various points in the red salmon life history (Thompson, 1953).

The Kvichak River program began under the general direction of Dr. W. F. Thompson; project leader since 1956 has been H. D. Smith. The smolt enumeration program was supervised in 1955 by Dr. R. L. Burgner, in 1956 and 1957 by D. W. Linn, and in 1958 and 1959 by the author. Records and preliminary unpublished

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Note.—The author is presently with the Fisheries Research Institute, College of Fisheries, University of Washington, Seattle 5, Washington.

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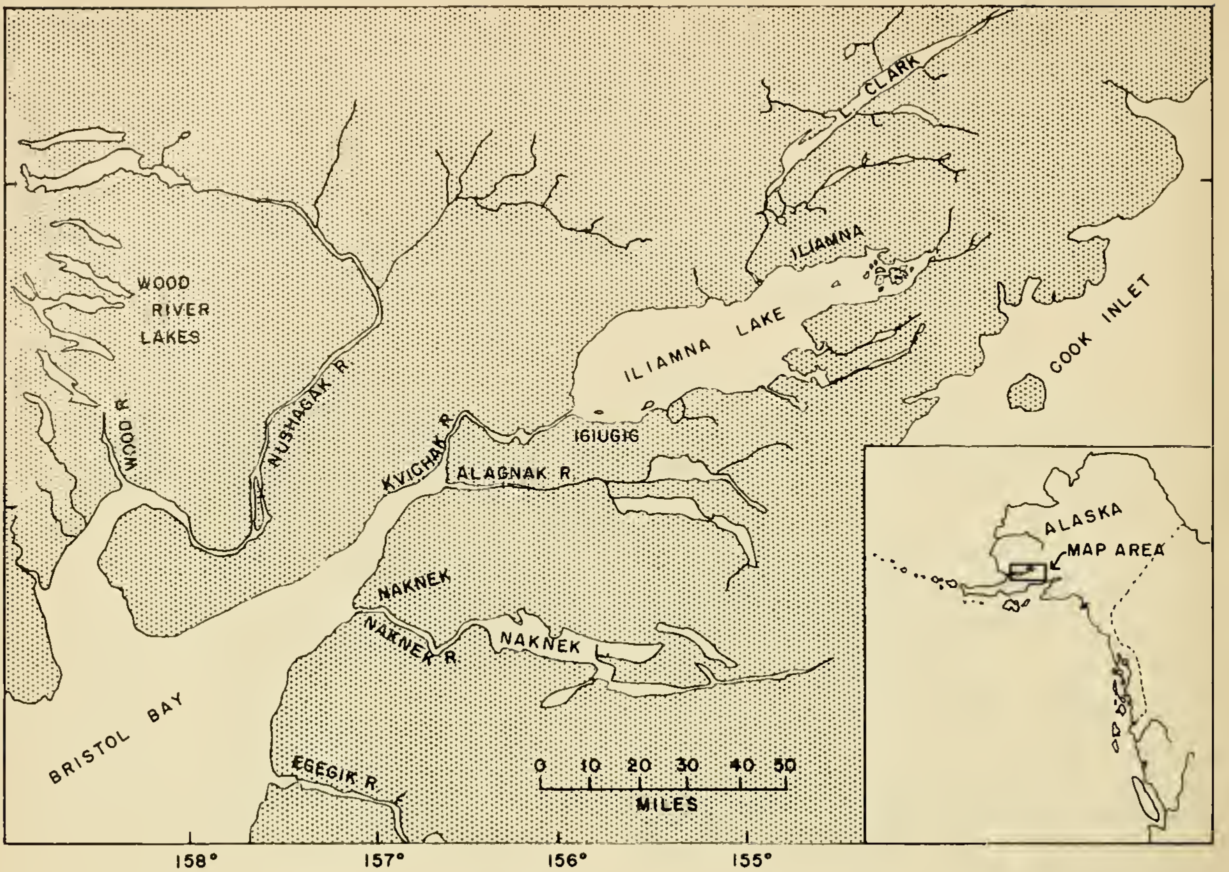

FIGURE 1.—Kvichak River system, Bristol Bay, Alaska.

reports of the Kvichak smolt studies are on file at the Fisheries Research Institute.

Credit for the development of most of the gear and methods used in this study is due Drs. W. F. Thompson, R. L. Burgner, and Ted S. Y. Koo, of the Fisheries Research Institute. The developmental work was conducted before 1951 at Mosquito Point, on the Nushagak River system, and was financed by Alaska Salmon Industry, Inc.

Unpublished reports were written by Dr. R. L. Burgner and D. W. Linn for the Kvichak smolt studies of 1955 and 1956, and the author has used freely and without reference the information from these reports.

Dr. O. A. Mathisen critically reviewed this paper and made helpful comments on the presentation of the data. The manuscript was edited by Drs. W. F. Royce, Ted S. Y. Koo, R. L. Burgner, and J. P. Harville, and H. D. Smith and J. F. Roos.

Appreciation is extended to all Fisheries Research Institute staff members, past and present, permanent and temporary, who were involved in collection of data.

DETERMINING RELATIVE SMOLT ABUNDANCE

Fyke-Net Design

The rigid frame of the fyke net used in this study measured 4 feet by 4 feet. The body of the net tapered from the frame to a single rectangular funnel 2 inches by 10 inches at the throat (fig. 2). A second funnel of the same dimensions was located in a detachable cod-end section, which facilitated emptying the catch. The net had two wings, each 10 feet long and 4 feet deep, with appropriate cork and lead lines. The two wings were held open by the force of the river current and two connecting spacer lines allowed the net to fish a consistent 9-foot wide section of the river. The net was made of

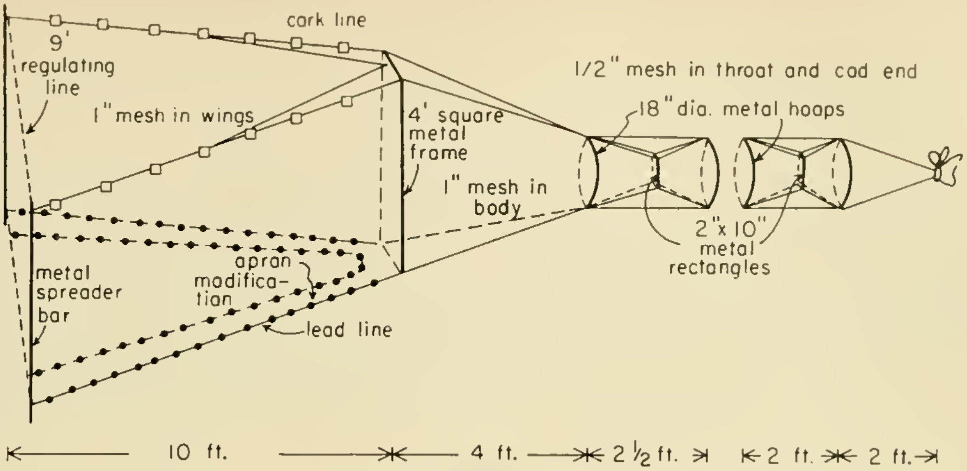

FIGURE 2.—Fyke net used in Kvichak River for assessing red salmon smolt abundance, 1955 through 1959.

knotted cotton webbing; the wings and body of 1-inch mesh (stretched measure) and the remainder of the net of ½-inch mesh. The fyke net is shown anchored in place in the river in figure 3.

Fyke-Net Site

Smolts contributed by both Iliamna Lake and Lake Clark must descend the Kvichak River on their way to the sea. The upper 4 miles of river from Iliamna Lake to Kaskanak Flats offer the

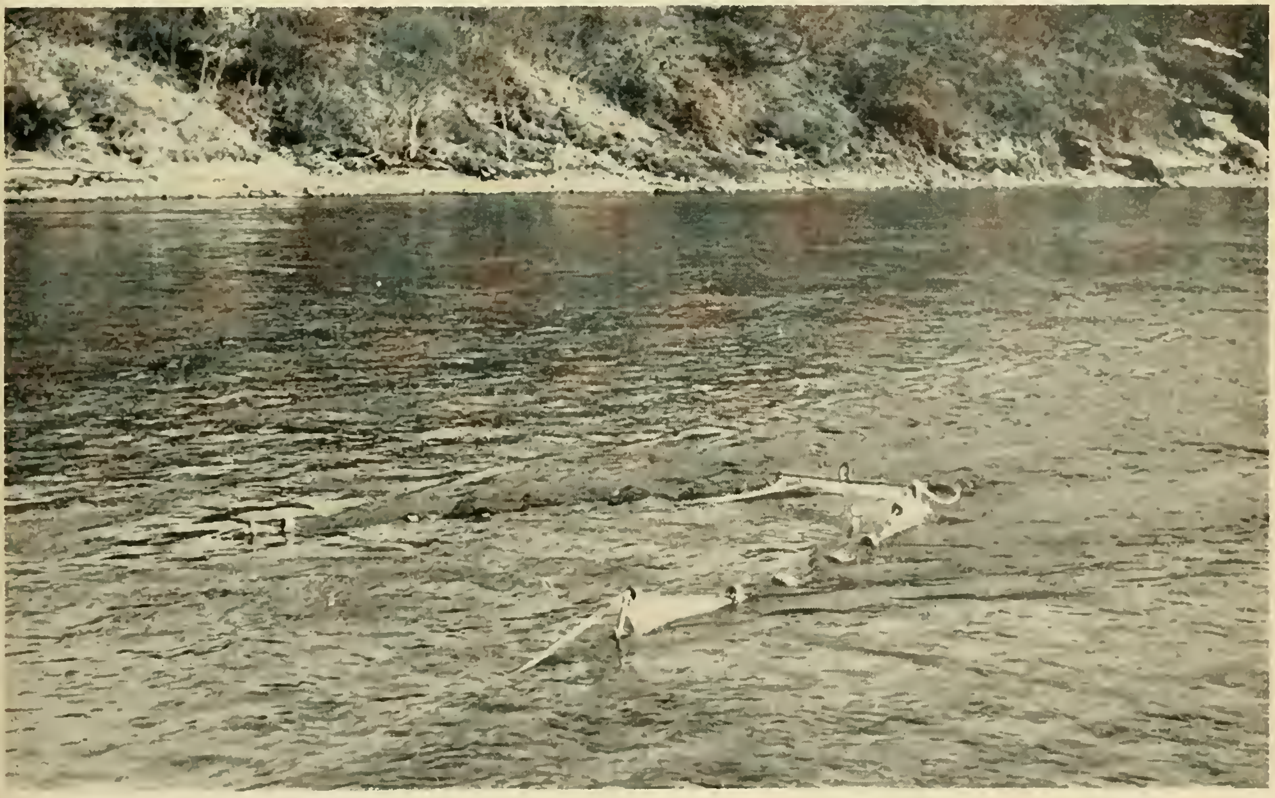

FIGURE 3.—Fyke net anchored in fishing position in the Kvichak River. (Photo by C. D. Becker.)

best fyke-netting sites. Here the river varies in width from about 400 feet to 1,000 feet, with depths to more than 15 feet and surface water velocities to at least 8 feet per second. The bottom consists mostly of gravel less than 4 inches in diameter. The riverbanks are steep because of the erosion that occurs nearly every year during high water. The river downstream from the Kaskanak Flats is affected by tides, causing variable water velocities unfavorable for fyke netting.

The index site (site B) used for smolt enumeration was approximately 4 miles downstream from the outlet of Iliamna Lake. Two other sites designated A and C were ½ mile and 2 miles downstream from the outlet (fig. 4). At the index site the river forms two channels, 570 feet wide and 225 feet wide. The fyke net was set on a submerged, slightly sloping gravel bar near the center of the main channel. This gravel bar extends at the same depth for at least 100 yards above and below the index site.

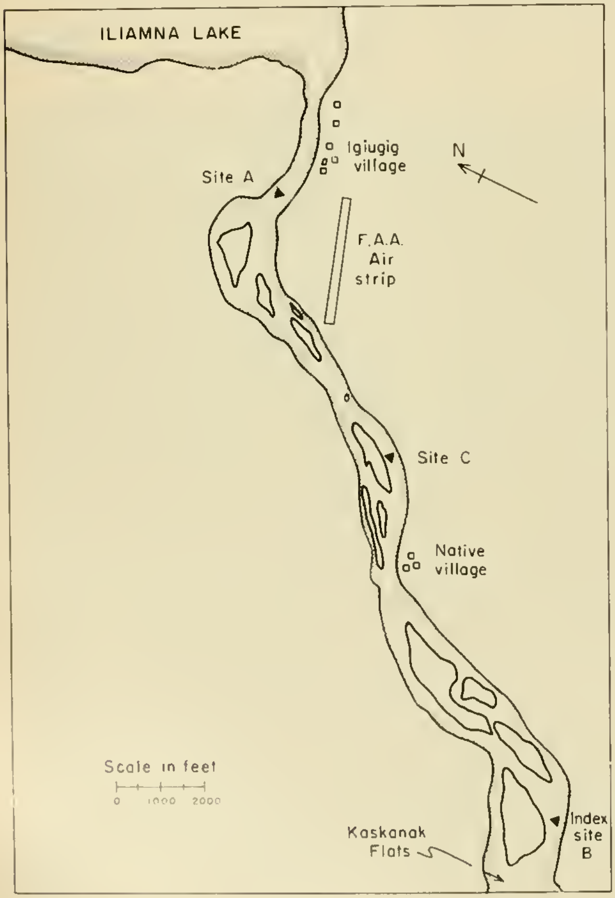

Figure 4.—Fyke-net sites A, B (index), and C, Kvichak River. (Map by D. W. Linn.)

Fyke-Netting Procedure

The fyke net was set before 2200 hours each night and tended from a 20-foot skiff by two or more men. To check the net, the cod end was first raised out of the water by one man. In this position the throat of the net was closed to the passage of fish. The cod end with the catch was detached by removing a single locking pin and an empty cod end immediately put in place and lowered into the water to continue fishing.

The second man pulled the release cord or zipper on the cod end and spilled the catch into a large weighing basket that was immersed in a tub of water. This weighing basket was then removed from the tub and hung on a spring balance of 40-pound capacity, suspended from a weighing stand in the skiff. The weighing basket was allowed to drain about 10 seconds before the weight of the fish and the time of catch were recorded. During peak migration the fish weighed about 20 pounds at a net check. Immediately after being weighed, the fish were returned to the river. Elapsed time for a net check was less than 30 seconds. The number of fish in a 1-pound sample was usually counted four times an hour and the number was used for conversion of total weight of fish to total number.

To avoid excessive mortality during periods of heavy migration, the net was checked as the fish accumulated. In an extreme instance in 1958 it was necessary to check the index fyke net nearly twice a minute. When the migration was very light, the net was checked every hour.

Fishing Season

The experimental fishing season during this study began in the spring before any smolt migration takes place and continued until only a few fish were caught each day. The smolt migration started after ice breakup (fig. 5) and following a rapid rise in water temperatures in Iliamna Lake.

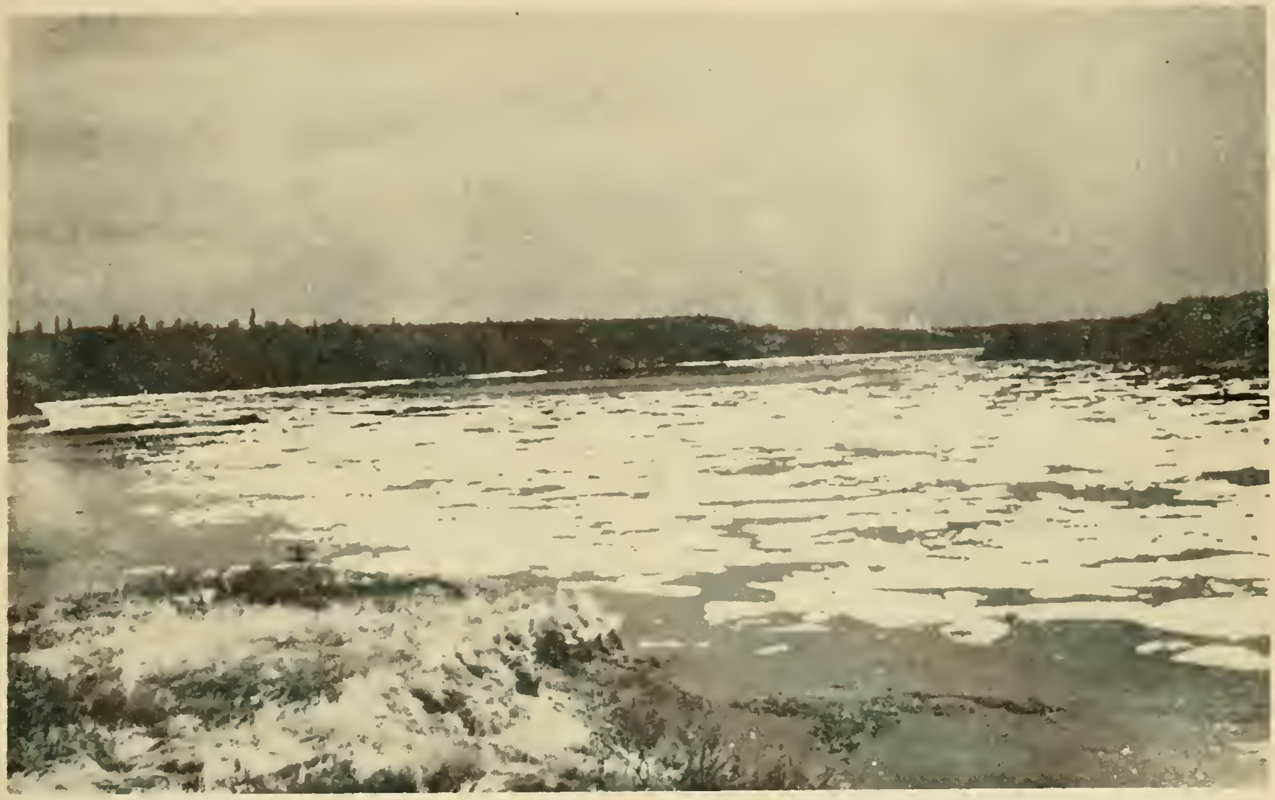

FIGURE 5.—Ice floes in the Kvichak River. (Photo by C. D. Becker.)

Daily Fishing Period

The smolt index was based on the total catch of the fyke net from 2200 to 0100 hours. This 3-hour period was selected on the basis of experience in the Nushagak system, where most of the smolts leave the lake during the darkest hours. The same nightly concentration of migration was found in the Kvichak River during 24-hour periods of fishing, as shown later.

River Conditions and Fyke-Net Efficiency

Water velocity.—Desirable surface-water velocity for fyke netting in the Kvichak River is 3 feet per second or more. This velocity is presumed necessary to prevent size selectivity, or larger fish evading the net. Net selectivity influenced by water velocity in the Kvichak River during 1955 was illustrated by two nets fished side by side at site A. The net in faster water, 3.1 feet per second, caught a greater poundage and larger-sized fish than the net in water of 2.4 feet per second velocity (fig. 6). A second test for size selectivity caused by similar water velocity was also made at the index site in 1955. The length frequencies of smolts taken during this test, in which two nets were fished side by side, are shown in figure 7. Both nets, fished in a current velocity of approximately 3.5 feet per

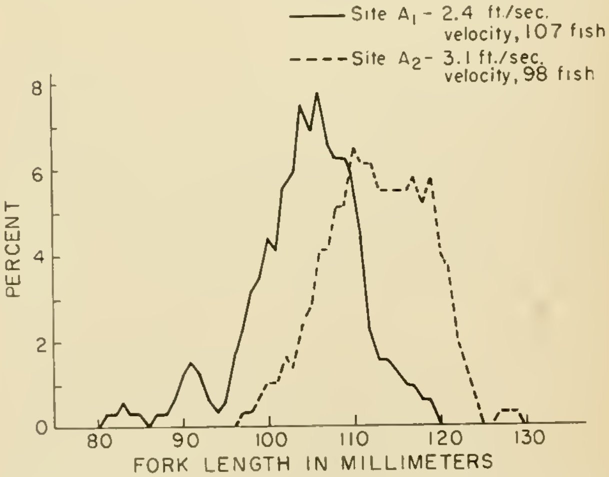

FIGURE 6.—Length frequencies of smolts captured in high and low velocity waters near site A from 2150 to 2210 hours, June 2, 1955. (Frequencies are smoothed by moving averages of threes.)

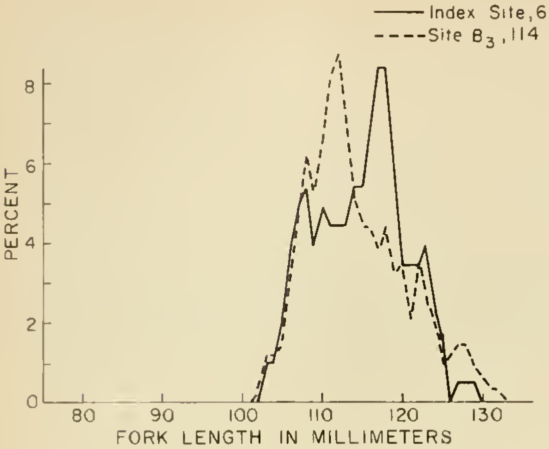

FIGURE 7.—Length frequencies of smolts captured in waters of similar velocity (approximately 3.5 feet per second) near index site from 2200 to 2212 hours, June 4, 1955. (Frequencies are smoothed by moving averages of threes.)

second, captured fish of comparable size. Water velocities at the index site were measured carefully with a Gurley current meter at least once each year during this study and varied little (table 1).

TABLE 1.—*Middepth water velocities at the index fyke-net site on Kvichak River*

Year	Date	Velocity (ft. /sec.)
1956	June 21	3.5
1957	June 21	3.6
1958	May 17	3.5
1959	May 29	3.4

Channel changes.—Changes in river depth or width in the vicinity of the index fyke-net site could radically affect the migration path of smolts and thus influence fyke-net catches. However, no appreciable changes in the contour of the river bottom at the index site have been detected on maps prepared each year by the method of plane table mapping and sounding (fig. 8).

Water depth.—Water depth for effective fyke netting in the Kvichak River is fixed at from 3.5 to 4 feet. At a greater depth some fish escape over the wings and center of the net, since the net must rest on the river bottom at all times to prevent fish passing beneath it.

Changes in water depth of the Kvichak River have followed the same pattern each year of this study. Water depth is at a minimum in spring and reaches a maximum in late summer or early autumn. Increased water discharge results from melting snow and glaciers or from rainfall. The annual range and increase in water depth as measured at the Igiugig gaging station during the period of fyke netting are shown in table 2. Fluctuations in water depth have been proportionate between the gaging and fyke-netting sites each year. Changes in water depths necessitate shifting the fyke net periodically to optimum depth during the smolt migration.

TABLE 2.—*Annual water-depth ranges and increases in the upper Kvichak River*

Year	Observation dates	Comparative range (in inches)	Increase (in inches)
1955	May 29 to June 30	11 to 24	13
1956	May 18 to June 30	13 to 26	13
1957	May 8 to June 30	0 to 26	26
1958	May 4 to June 30	7 to 37	30
1959	May 23 to June 30	0 to 14	14

NOTE.—All water depths are based relatively on the lowest recording (in 1957), which is assigned the value of 0. The permanent water level gage is about 1 mile downstream from the outlet of Iliamna Lake.

Debris.—Net-clogging debris in a river can be a variable factor in operation of fyke nets. Efficiency of clogged nets was tested by Dr. Koo and the author in the Ugashik River system of Bristol Bay in 1956 (table 3). On even-numbered nights one net was used during the entire fishing period, and on odd-numbered nights a clean net was substituted midway in the fishing period at 2000 hours. Tests on nights when the net was not replaced indicated

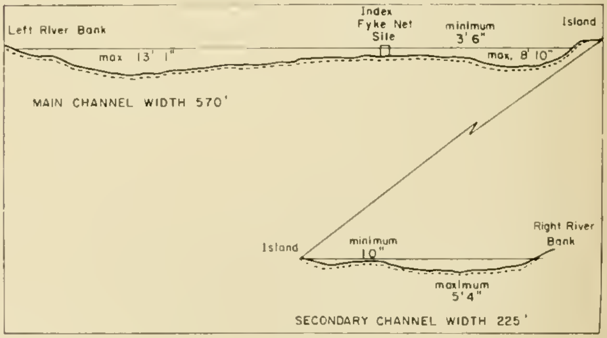

FIGURE 8.—Typical river bottom contour at index site, Kvichak River, June 23, 1958. (Water-gage reading, 32 inches; ratio of depth to width is drawn as 2 to 1.)

TABLE 3.—*Comparison of hourly fyke-net catches of smolts on one-net days (severe clogging) and two-net days (reduced clogging), Ugashik River, 1956*

Date	Hourly catch										
	1500–1600	1600–1700	1700–1800	1800–1900	1900–2000	2000–2100	2100–2200	2200–2300	2300–2400	2400–0100	Total
Two-net days:[1]											
June 1	0	2,000	2,858	409	280	1,376	18	208	132	495	7,776
3		9	2	123	10	0	158	4,576	1,056		5,934
5		0	45	0	0	0	0	17	3		65
7		361	16	7	0	168	249	137	567		1,505
9	20	21	101	1	150	0	0	1	139	43	476
13	17	131	9	0	0	1	1	24	38	84	305
15	0	0	31	120	1	8	0	0	23	70	253
17	0	0	0	0	0	0	0	121	89	3	213
Total	37	2,522	3,062	660	441	1,553	426	5,084	2,047	695	16,527
Percent	0.2	15.3	18.5	4.0	2.7	9.4	2.6	30.8	12.4	4.2	100.1
One-net days:											
May 31		624	1,656	1,200	3,096	63	909	23	155		7,726
June 2		1,281	656	390	1,722	492					4,541
4		13	2,005	0	0	1,417	5	12	8		3,460
6		0	0	1	0	8	0	1			10
8		384	1	0	86	0	2	0	49		522
10		160	540	38	140	5	3	2	7		895
12		0	4	3	5	2	1	37	18		70
14		1	221	206	199	720	58	68	19		1,492
16		0	0	0	1	357	25	1	5		389
18		0	0	0	0	15	0	6	16		37
Total		2,463	5,083	1,838	5,249	3,079	1,003	150	277		19,142
Percent		12.3	26.6	9.6	27.4	16.1	5.2	0.8	1.4		100.00

[1] Net change occurred at 2000 hours.

that the fyke-net catch decreased gradually with clogging for a period of 5 hours, after which few fish were caught. On nights when the clogged net was replaced with a clean net, the greater efficiency showed in an increased catch.

The most troublesome form of debris in the Kvichak River was a colonial diatom (*Gomphonema* sp.) which drifted in ribbonlike streams from Iliamna Lake whenever a moderate to strong wind prevailed down the lake. Debris of terrestrial origin, grass and leaves, became an occasional nuisance late in the season with the higher water levels. During periods of abundant debris it was necessary to change the nets frequently or to clean them while in fishing position.

DETERMINING SMOLT AGE

Sampling Procedure

From 1955 through 1957, representative 2-pound samples of smolts were taken from the fyke-net catches in approximate proportion to the size of the migration. On nights of heavy migration several samples were taken, and on nights of light migration one or no sample was taken. In 1958, 2-pound samples, taken in ½-pound lots each 15 minutes, were collected during each hour, provided adequate numbers of fish were available. The sampling procedure in 1959 was similar to that of 1958 except that 1-pound samples rather than 2-pound samples were taken. The fish included in all samples were taken randomly from the weighing basket to prevent size selection resulting from possible stratification. The samples of live fish were transferred to separate containers, which were 10-gallon milk cans or boxes placed along the riverbank in slow-moving water. The milk cans were partly screened on the sides and the boxes were made of ⅛-inch saran screen.

During the first 3 years of the investigations, samples were processed each morning; during 1958 and 1959, within 5 hours of capture. The change was made in 1958 to prevent mortalities that occurred in the earlier years from holding the fish overnight.

Length-Frequency Samples

The two important age groups of smolts in the Kvichak River, those spending one or two winters in fresh water, can nearly always be separated by length alone. Therefore, all fish in each sample were measured and the length-frequency method of age determination was employed.

Fish in groups of 10 to 15 were anesthetized in urethane[1] or chlorotone, measured from the tip of the snout to the fork of the tail, and returned to a container of fresh water to revive. Each length was tallied together with information identifying the sample. At a later date all length-frequency tabulations for 1 day were weighted according to the magnitude of the fyke-net catches during the daily 3-hour index period and combined in a composite season sample.

Scale Samples

Ages determined from length frequencies were verified from scale samples. Scale samples were taken from fish used in the length-frequency measurements, and the fish selected for scale samples were immediately preserved in 5-percent formalin. Several weeks after preservation, the fish were remeasured and the scale samples removed. Shrinkage of preserved specimens was adjusted by a shrinkage factor determined by measuring individual fish before and after their preservation. Shrinkage from live length varied from 3 to 7 percent, depending on the length of the fish, or about 4 millimeters. Four to eight scales were taken from each fish from immediately above or below the lateral line and between the dorsal and adipose fins. These scales were mounted in a spread pattern on a 1- by 3-inch glass slide. Scales from eight fish were mounted on a slide, with the length of each fish recorded on the slide label. The scales were covered with a second glass slide and the two slides taped together.

All scales were studied to determine number of annuli and amount of spring growth since formation of the last winter annulus. Spring growth does not appear on the scales of smolts that migrate soon after lake ice breakup, but it becomes apparent about midway through the migration season and the growth increases during the summer.

ABUNDANCE OF SMOLTS

The annual Kvichak River smolt index was based on the number of fish captured in a single fyke net fished each year of the study under similar fishing conditions and for the duration of the migration. This method was designed to detect fluctuations in the number of smolts from year to year. The number of smolts and calculated index values for the 5 years of the study are presented in table 4. The daily smolt catches each year are shown in appendix tables 1 through 5.

Table 4.—*Indices of smolt abundance in the Kvichak River*

Year	Number of smolts	Index value [1]
1955	214,000	11.2
1956	64,000	3.3
1957	25,000	1.3
1958	1,913,000	100 0
1959	1,643,000	85.9

[1] The total number of smolts caught in 1958 has been arbitrarily assigned the base value of 100.0.

Some adjustments of each year's total catch have been necessary. For the first 3 years of the study, some smolt catches from secondary net sites A and C were included to obtain the index value. The use of these sites was necessary because ice in the river prevented fishing at the index site early in the season and because the biologists who did the counting were involved with other duties late in the season. During 1955 and 1957, the catches from net-sites A and C were included when the two nets were contributing less than 7 percent of the season's catch. During the period of the ice flow in 1956 a substantial migration was detected at site A; and, consequently, an evaluation of these catches in terms of principal index-site catches was necessary. This evaluation was made on the basis of simultaneous fishing at the index site and site A for 4 days, from June 7 through June 10 (table 5). The ratio of catches of site A to those of the index site for the 4 days was

Table 5.—*Simultaneous smolt catches at site A and at the index site, 1956*

Date	Catch at—	
	Site A	Index site
June 7	874	9,449
June 8	16	4,127
June 9	8	1,851
June 10	0	115
Total	898	15,542

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[1] Urethane has not been used extensively since reports of its carcinogenic effects were published.

0.06:1.00, and this ratio was applied to the catches obtained at site A before June 7 to estimate the index catches for this early period. The estimated index catches for 1956 are shown in appendix table 2.

During each year's smolt migration some hours and days of fishing were missed because of ice in the river or failure of the fyke-net anchors. Estimates of the number of fish passing the net site during hours not fished have been calculated on the basis of the average catch of the preceding and following hours. Estimates for days missed have been made by averaging the catches of the preceding and following days. Estimates for fishing hours missed have never exceeded 8 percent of the season's catch, and estimates for days missed have never exceeded 2.5 percent of the season's catch. The maximum estimate of hours missed was for the 1955 run and the maximum estimate of days missed was for the 1957 run.

During the peak of the 1959 migration, the cod end was placed on the net for 5 minutes of each 15 minutes fished and occasionally 5 minutes of each 30 minutes fished. The catches were multiplied by 3 or 6, as appropriate, for estimates of the 15- and 30-minute periods. This subsampling reduced handling of the fish and consequent injury to them. The estimates from the intermittent fishing in 1959 are considered reliable because of the homogeneity of catches noted in 1958 during periods of continuous net checking at the peak of migration. To test this homogeneity for 1958, all combinations of every third 5-minute catch (for the estimate of the 15-minute periods of fishing in 1958) were compared with the total of all consecutive 5-minute catches (total of 98), and the maximum error was found to be about ±0.5 percent. When each combination of every sixth 5-minute catch (for the estimate of the 30 minute periods) was related to the total catch, the maximum error was less than ±4.0 percent.

Timing of Migration

The timing of the Kvichak River smolt migrations is depicted by the annual cumulative catch curves (fig. 9). Each spring the migration started near the final day of ice flow in the Kvichak River (table 6) and continued through June or early July. The 1958 smolt migration is the earliest on record and corresponds to the early breakup of lake ice for that year.

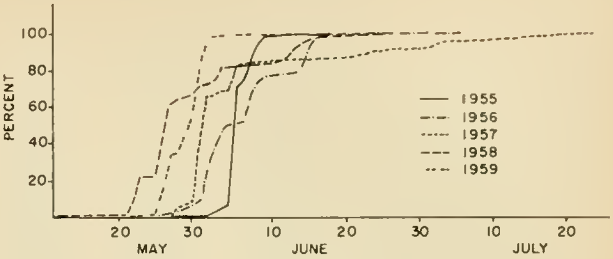

FIGURE 9.—Cumulative daily smolt catches at the index site in the Kvichak River, 1955 through 1959.

TABLE 6.—*Final day of ice flow in the Kvichak River*

Year	Date
1955	June 3
1956	June 6
1957	May 27
1958	May 9
1959	May 27

Each year the peak period of smolt abundance has been less than 2 weeks in duration (table 7). In the future this short period of major abundance can probably be used to reduce the effort previously necessary for smolt enumeration. Fyke netting can be started near the time of ice breakup and be continued only through the peak period of migration.

TABLE 7.—*Periods of peak catches of smolts in the Kvichak River*

Year	Total sampling period		Period of peak catches		
	Date	Number of days	Date	Number of days	Percent of season's catch
1955	May 28 – June 27	31	June 4 – 9	6	94
1956	May 24 – July 4.	42	June 1 – 9, 14 – 16.	12	88
1957	May 28 – July 24.	38	May 28 – June 6.	10	84
1958	May 10 – July 5.	56	May 22 – June 3.	13	80
1959	May 23 – June 28.	36	May 26 – June 2.	8	98

Hourly Index Catches

The hours of largest smolt catch for each year are shown graphically in figure 10. In 1955 and 1956, the catches were largest from 2300 hours to midnight; during 1957 and 1958

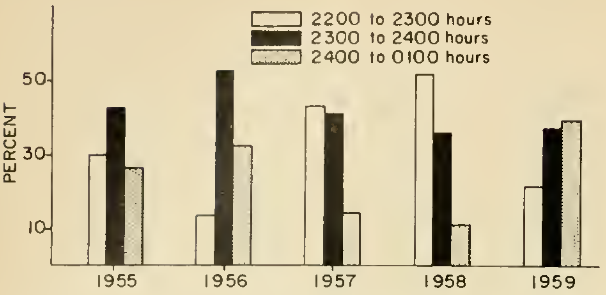

Figure 10.—Annual smolt catches, by hour, at the index site, 1955 through 1959.

they were largest from 2200 to 2300 hours; during 1959 they were largest from midnight to 0100 hours. The change in the hour of peak catches probably was related to the onset of darkness, which seems to promote smolt migration (Hoar, 1954). Darkness in the Kvichak system in May normally occurs about 2200 hours and in June about 2300 hours. During 1957 and 1958 the migration took place primarily in May, and therefore the early hour of peak migration. The 1959 migration also occurred in May but during this year the May nights were exceptionally clear and light. The 1955 and 1956 migrations occurred primarily in June which accounted for the later hour of peak migration than in 1957 or 1958. Extended fishing in 1958 and 1959 from 2100 to 0200 hours for most of the season established one index hour for each of these 2 years as the hour of greatest abundance (table 8).

Table 8.—*Hourly smolt catches at index site, May 10 to July 5, 1958, and May 27 to June 2, 1959*

Item	2100–2200	2200–2300	2300–2400	2400–0100	0100–0200	Total
1958:						
Catch	715,990	997,855	700,966	213,946	146,331	2,772,088
Percent	26	36	25	8	5	100
1959:						
Catch	76,071	293,069	503,532	578,690	461,214	1,912,576
Percent	4	15	26	31	24	100

24-Hour Fishing

Operation of the fyke net in several 24-hour periods was carried out only during 1957 and 1958 and only during a few of the peak days of migration (fig. 11; appendix tables 6 and 7). For purposes of analysis, the 24-hour periods were divided into six 4-hour intervals. In 1957, the year of smallest migration, more than 91 percent of the fish caught during the 12 days of round-the-clock fishing were taken from 2200 to 0200 hours (see fig. 11; appendix table 6). In 1958, the year of largest migration, only 62 percent of the catch was taken during this same 4-hour period in 9 days of 24-hour fishing (appendix table 7).

During 1959, many visual observations on a 24-hour basis revealed considerable migration outside the 3-hour period (2200–0100 hours). The cumulative number of fish migrating at a time other than the index period creates an underestimate of smolt abundance based on the index fishing period alone. No adjustment for daylight migration has been made for 1958 and 1959. Index fyke netting on a 24-hour basis, especially during years of large migration, is desirable in the Kvichak River system. Perhaps an automatic electronic counter can be used to reduce the cost of operation for this extended fishing.

Smolt Catches at Adjacent Net Sites

In 1955, two fyke nets were fished side by side, 50 feet apart, in the immediate index area for 4 days near the period of peak migration to obtain information on the variation that might be expected in catches from nets fished in the general area of the index site. The hourly catches (table 9) showed some variation, which

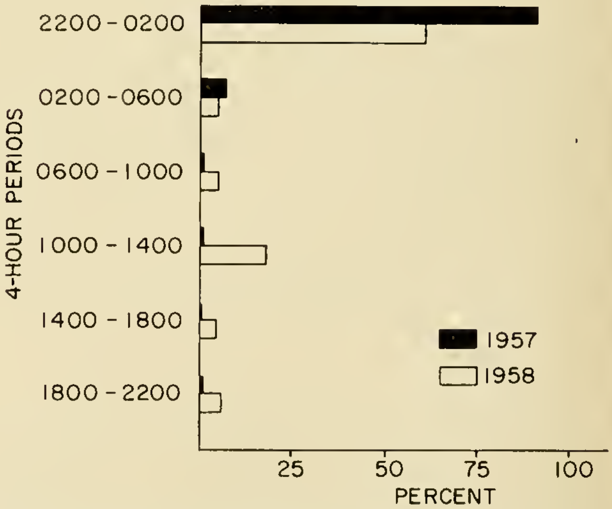

Figure 11.—Smolt catches on days of 24-hour fishing at the index site, 1957 and 1958.

TABLE 9.—*Comparative hourly catches of smolts at index site and at site B_4, June 7–10, 1955*

Date and site	2200–2300	2300–2400	2400–0100	Total
June 7:				
Index	1,824	20,482	2,020	24,326
B_4	1,577	11,926	2,100	15,603
June 8:				
Index	5,327	7,973	3,440	16,740
B_4	7,492	8,792	2,815	19,099
June 9:				
Index	2,295	3,005	2,984	8,284
B_4	2,600	9,978	3,686	16,264
June 10:				
Index	0	45	0	45
B_4	0	0	3	3
Total:				
Index	9,446	31,505	8,444	49,395
B_4	11,669	30,696	8,604	50,969

tends to average out over a period of time, indicating that nets fished in the general index area should sample effectively.

Smolt Catches at Distant Net Sites

In 1957 and 1958, efforts were made during most of the season to estimate the variability in smolt catches by fishing the index site simultaneously with site C, which is located 2 miles upstream (fig. 12). The daily smolt catches of the two nets for 1957 were similar, as were the total catches. The total catch at the index site was 23,000 fish and at site C, 19,000 fish (appendix table 13). These comparable catches suggest that both nets were fishing the same population at about the same rate during this year of relatively small abundance. In 1958, a year of much greater smolt abundance, the daily catches of the same two nets simultaneously reflected the fluctuations in the smolt migration but with less fidelity than in 1957 (fig. 12; appendix table 14). The total catch at site C in 1958 was only 40 percent as large as the catch at the index site. The difference in total numbers was due to much greater catches at the index site on the 5 days of heaviest migration. Visual observations and actual catches during these 5 days indicated that a large proportion of the smolt migration passed the upriver site C before the net-setting time.

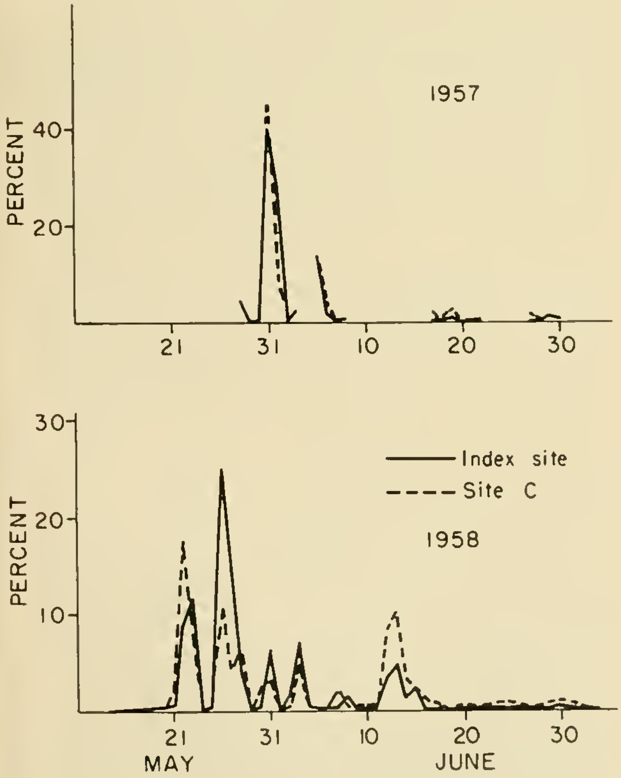

FIGURE 12.—Comparative smolt catches at index site and site C, Kvichak River, 1957 and 1958.

AGE COMPOSITION OF SMOLTS

For simplicity of analysis, samples used in smolt age determinations were restricted to those collected on days of major catches. The percentage of each year's smolt catch represented by the samples is shown in table 10.

Age analysis has been directed toward identification of two smolt groups only: fish which have spent one winter in fresh water, and fish which have spent two winters in fresh water. According to scale samples collected since 1955, smolts that have spent three winters in fresh water and fry (no winters) have been rare. Their rarity has been further verified by analysis of about 6,500 adult red salmon scales that were taken from escapement samplings at the outlet of Iliamna Lake from 1955 to 1959.

TABLE 10.—*Smolt age-determination samples from the Kvichak River*

Year	Number of days of sampling	Fish caught during days of sampling	
		Number	Percent
1955	7	210,000	98
1956	15	[1] 31,000	96
1957	9	21,000	84
1958	13	1,794,000	94
1959	8	1,608,000	98

[1] The samples were taken at both site A and the index site; therefore, the actual catches of these two sites, during nights of sampling, were added to obtain the 31,000.

Analysis of these adult scales by Dr. Koo indicated that all smolts migrated before they had spent three winters in fresh water. In 1955 only 0.2 percent migrated from the lake as fry; in other years, no fry migrated.

The proportions of Kvichak River smolts in the two age groups during the 5 years of study are illustrated in the length-frequency curves of figure 13. The tabulated information regarding the daily sample size, the proportion of fish having spent one winter in fresh water, and the weighting values are shown in appendix tables 8 through 12.

Two relationships are apparent from these data. First, a definite trend is present in 1955 through 1958 from fish that spent two winters in fresh water to an increasingly dominant proportion of fish that spent one winter in fresh water. Then a complete reversal occurs in 1959 with dominance of the older fish. Additional years of data are necessary to establish the presence or absence of cyclic changes. Second, the modal length of the fish is related to population density in the lake system before migration. In 1958, the year of greatest abundance in Iliamna Lake, the mode of the fish that spent one winter in fresh water was about 1 centimeter less than that of the one-winter fish of other years. The same has been true of the fish in the older age group in 1955 and 1959, the next years of greater smolt abundance. The length modes of both age groups in 1956 and 1957, years of low abundance, have been larger or have been shifted to the right of the modes of 1955, 1958, and 1959. This same relationship has been reported in the Lake Dalnee red salmon smolts by Krogius and Krokhin (1948).

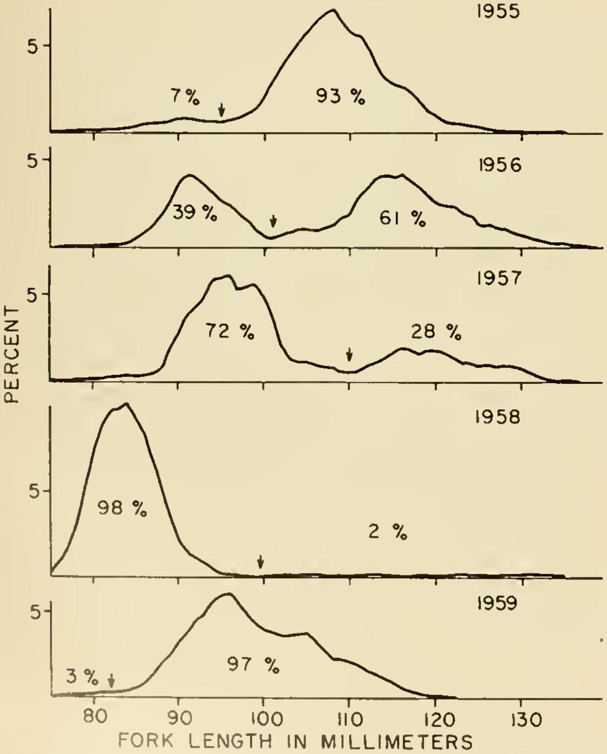

FIGURE 13.—Composite length frequencies of smolts, 1955 through 1959. (Each daily sample is weighted by magnitude of the fyke-net catches for that day. Total frequency for each year is smoothed by moving averages of threes. The arrows indicate the division point between age groups, as verified by scale samples.)

The relation between the smolt index catch by age groups and the magnitude of the parent escapement for each year of observation is shown in table 11. It is concluded from the data that large escapements have produced large smolt migrations, and small escapements have produced small smolt migrations.

Smolt Sizes at Adjacent Net Sites

In 1955 a comparison of smolt sizes was made in the simultaneous catches of two nets set side by side, 50 feet apart, at the index site. The

TABLE 11.—*Kvichak River parent escapements and resulting smolt catches*

Year	Number of fish in parent escapement [1]	Smolt catch		
		Age group [2]	Year	Number of smolts
1952	5,970,000	1	1954	No data.
		2	1955	195,000
1953	321,000	1	1955	19,000
		2	1956	39,000
1954	241,000	1	1956	25,000
		2	1957	7,000
1955	251,000	1	1957	18,000
		2	1958	39,000
1956	9,443,000	1	1958	1,874,000
		2	1959	1,591,000
1957	2,843,000	1	1959	47,000
		2	1960	432,000

[1] 1952-1954 escapements estimated from spawning-ground surveys by J. R. Gilbert and H. D. Smith. Since 1955, escapements estimated by daily tower counts at Igiugig.

[2] Number of winters the smolts spent in fresh water.

results are shown as length-frequency curves in figure 14. The similarity between the two nets in sizes of fish caught indicate that nets fished in the area bordered by the index and B_4 sites should sample reliably. The length-frequency curves presented in figure 7 also show similarity in the sizes of fish taken by two nets fished side by side.

Smolt Sizes at Distant Net Sites

Smolt samples taken in 1957 and 1958 during the simultaneous fishing of two nets, one 2 miles upstream from the other (fig. 15; appendix tables 10, 11, 15, and 16), show similarity of length frequencies and age composition and indicate that the nets were intercepting the same smolt population.

Verification of Fresh-Water Age

It is reasonable to assume that if the age composition of the smolts is reliable, then the fresh-water age composition of the adults that return after two or three winters in the ocean should be similar to that of the smolts. This comparison is made on the assumption that the marine survival rate is relatively constant for one-winter and two-winter fish. Only the adult samples taken at the Igiugig tower sites were used in this comparison, because samples from the commercial catch include fish bound for adjacent rivers in the Naknek and Egegik districts as well as the Kvichak River. The percentages of the two age groups of smolts in the 1955, 1956, and 1957 migrations, and the percentages of the various age groups of adults that returned from these smolt migrations are shown in table 12. This good relationship of smolt age to adult fresh-water age indicates the method for smolt age determination is valid.

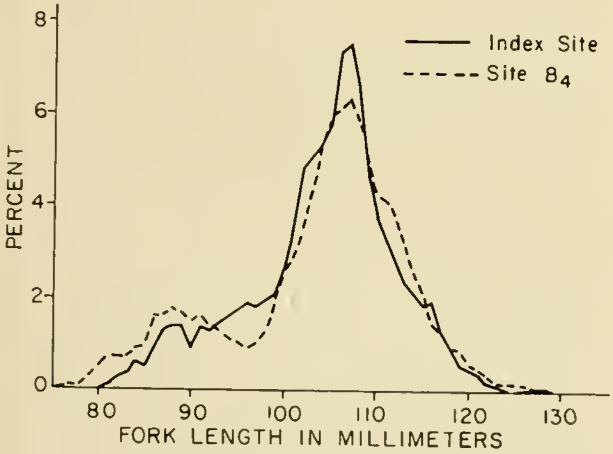

FIGURE 14.—Length frequencies of smolts captured at the index site and site B_4 between 2200 and 0100 hours, June 7 and 8, 1955. (Frequencies are smoothed by moving averages of threes.)

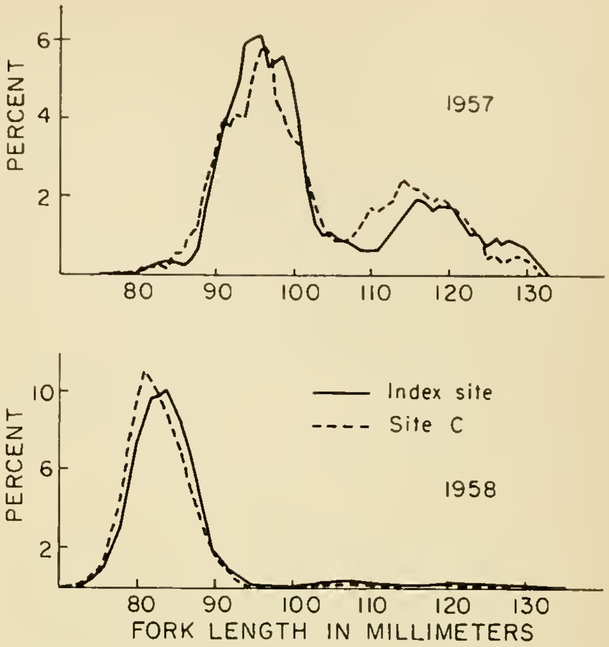

FIGURE 15.—Comparative smolt length frequencies, index site and site C, 1957 and 1958. (Each daily sample was weighted by the magnitude of the smolt catch for that day. Frequency for each year is smoothed by moving averages of threes.)

TABLE 12.—*Age groups (in percent) of smolts in migrations of 1955, 1956, and 1957 and of adults returning 2 and 3 years later*

Smolt migration [1]	Percent of sample	Adult returns			
		2 years later		3 years later	
		Age group [2]	Percent	Age group [2]	Percent
1955:					
Age-group 1	9	4_2	3	5_2	8
Age-group 2	91	5_3	97	6_3	92
1956:					
Age-group 1	37	4_2	24	5_2	31
Age-group 2	63	5_3	76	6_3	69
1957:					
Age-group 1	72	4_2	25	5_2	100
Age-group 2	28	5_3	75	6_3	0

[1] Age groups of smolts refer to number of winters the smolts spent in fresh water.

[2] Adult age determinations from escapement scale samples analyzed by Dr. Koo. Arabic figure refers to year in which fish returned as adults, and subscript figure refers to year in which fish migrated to sea.

The slightly increased percentage return of smolts that had spent two winters in fresh water probably could be expected because of their larger size and better chance of survival in the sea. This conclusion follows that of Foerster (1954), who showed a direct relation between marine survival and size of smolts. The discrepancy in age composition between the 1957 smolts and the adults returning in 1959 after two winters in the ocean could be due to inaccurate smolt sampling or to good survival conditions in the ocean. Good survival of fish spending two winters in the ocean was evident in nearly all districts of Bristol Bay in 1959.

DISCUSSION

The methods used in this study do not lead to a finite evaluation of smolt abundance and age composition. However, their reliability has been supported by most tests conducted during the past 5 years. The tests involved the simultaneous fishing of two nets side by side and two nets 2 miles apart up and down the Kvichak River, and the relating the age of the smolts to the fresh-water age of returning adults. It is important to note that the great differences in index values from year to year permit a large error in the accuracy of the method but the index method still enables detection of important changes in smolt abundance. Tremendous differences in abundance from year to year do occur, as is evident from the striking changes in the size of the adult population of Kvichak River red salmon (table 11). The large adult escapements have produced large smolt migrations and small adult escapements have produced small smolt migrations. Two extremes in the smolt index values are apparent for the past 5 years, the minimum represented by 1956 and 1957, and the maximum represented by 1958 and 1959 (table 4). The index of 1955 is nearly four times larger than the next smaller value (1956) but eight times smaller than the next higher value (1959).

The methods described in this paper have been shown to be reasonably accurate to date. Final evaluation of these methods, however, must wait until data are available on the return of adult salmon from a longer series of smolt migrations. Only after such an evaluation period can the estimation of the population variables and the prediction of subsequent adult returns be achieved with accuracy.

SUMMARY

The purpose of the smolt study, conducted from 1955 through 1959, was to provide an annual index of abundance and to determine the age and size composition of Kvichak River red salmon.

The relative index method used to assess smolt abundance was based on the season-long catch of a single fyke net set at the index site throughout the same daily fishing period (2200 to 0100 hours) and under similar river conditions each year. It was designed to determine major fluctuations in smolt abundance from year to year.

The annual indices of Kvichak smolt abundance were for 1955, 11.2; 1956, 3.3; 1957, 1.3; 1958, 100.00; 1959, 85.9. These index values are relative to the combined smolt catches of 1958, which were assigned a value of 100.0. The tremendous differences in smolt index values permit a large error in the accuracy of the method, but the index method enables the detection of important changes in abundance.

Large parent escapements have produced large smolt migrations and small parent escapements have produced small smolt migrations.

Weighted length-frequency samples, verified by scale samples, were used in age determination. Two predominant age groups of smolts occur in Kvichak River: those that have spent one winter in fresh water and those that have spent two winters in fresh water.

The smolt age composition for the 5 years indicated a trend toward cyclic variation and a relation of size to population density, smaller fish occurring during years of large abundance. The similarity of smolt ages with the fresh-water ages of returning adults supports the methods and results of age determination.

LITERATURE CITED

BURGNER, ROBERT L.

1958. A study of fluctuations in abundance, growth and survival in the early life stages of the red salmon (*Oncorhynchus nerka* Walbaum) of the Wood River lakes, Bristol Bay, Alaska. University of Washington, Seattle. 200 p. [Ph.D. thesis.]

FOERSTER, RUSSELL EARLE.

1929. An investigation of the life history and propagation of the sockeye salmon (*Oncorhynchus nerka*) at Cultus Lake, British Columbia. No. 3. The down-stream migration of the young in 1926 and 1927. Biological Board of Canada, Contributions to Canadian Biology and Fisheries, vol. 5 (new series), no. 3, p. 55–82. Ottawa.

1954. On the relation of adult sockeye salmon (*Oncorhynchus nerka*) returns to known smolt seaward migrations. Journal, Fisheries Research Board of Canada, vol. 11, no. 4, p. 339–350. Ottawa.

HOAR, W. S.

1954. The behaviour of juvenile Pacific salmon, with particular reference to the sockeye (*Oncorhynchus nerka*). Journal, Fisheries Research Board of Canada, vol. 11, no. 1, p. 69–97. Ottawa.

INTERNATIONAL PACIFIC SALMON FISHERIES COMMISSION.

1955. Annual report for 1954. Wrigley Print Co., Ltd., New Westminster, British Columbia. 42 p.

KROGIUS, F. V., and E. M. KROKHIN.

1948. Ob urozhainosti molodi krasnoi (*Oncorhynchus nerka* Walb.). [On the production of young sockeye salmon (*Oncorhynchus nerka* Walb.)]. Izvestiia Tikhookeanskovo Nauchno-Issledovatelskovo Instituta Rybnovo Khoziaistva i Okeanografii, tom 28, p. 3–27. [Translation by R. E. Foerster, 1958, Translation Series No. 109, Fisheries Research Board of Canada, Nanaimo, British Columbia.]

THOMPSON, WILLIAM F.

1953. Red salmon of the Nushagak. [Abstract]. *In* Science in Alaska, 1953. Proceedings of the Fourth Alaskan Science Conference, p. 89–90. [Fisheries Research Institute Circular No. 50 (revised 1955), University of Washington, Seattle.]

U. S. ARMY CORPS OF ENGINEERS.

1957. Harbors and rivers in southwestern Alaska. U.S. House of Representatives, House Document No. 390, 84th Congress, 2d Session, 89 p.

APPENDIX

APPENDIX TABLE 1.—*Kvichak River smolt catches, by site, day, and hour, 1955*

Site and date	2200–2300	2300–2400	2400–0100	Total [1]	Percent
Site A:					
May 28				36	0.02
29				18	0.01
30				114	0.05
31				91	0.04
June 1				12	0.01
2				8,148	3.81
3				450	0.21
Index site:					
June 4				8,106	3.79
5	40,573	54,422	39,084	134,079	62.75
6	5,590	938	1,661	8,189	3.83
7	1,824	20,482	2,020	24,326	11.38
8	5,327	7,973	3,440	16,740	7.83
9	3,952	3,005	2,984	9,941	4.65
10	0	45	0	45	0.02
11				10	0.01
12	30	0	1	31	0.02
13	0	277	329	606	0.28
14	27	2	3	32	0.02
15	4	32	4	40	0.02
16	0	5	3	8	0.00
17				376	0.18
18	118	183	180	481	0.23
19	5	36	28	69	0.03
20				45	0.02
21	0	5	5	10	0.01
22	54	45	2	101	0.05
Site C:					
June 23	214	121	100	435	0.20
24	477	217	224	918	0.43
25	48	84	69	201	0.09
26	6	16	2	24	0.01
27	0	0	2	2	0.00
Total	58,249	87,888	50,141	213,684	100.00

[1] For days where no hourly catches are given, the totals, in part, are based on fyke-net catches before or after the index hours during the same day.

APPENDIX TABLE 2.—*Kvichak River smolt catches, by site, day, and hour, 1956*

Site and date	2200–2300	2300–2400	2400–0100	Total [1]	Percent
Index site:					
May 24				0	0.00
25				155	0.24
26				1,019	1.59
27				328	0.51
28				803	1.26
29				1,278	2.00
30				499	0.78
31				1,261	1.97
June 1				11,779	18.44
2				6,632	10.38
3				6,632	10.38
4				1,485	2.32
5				933	1.46
6				449	0.70
7	1,113	3,556	4,780	9,449	14.79
8	325	1,126	2,676	4,127	6.46
9	498	1,093	260	1,851	2.90
10	0	0	115	115	0.18
11	103	35	0	138	0.22
12	9	5	3	17	0.03
13	32	26	25	83	0.13
14	1,692	789	610	3,091	4.84
15	731	4,804	1,391	6,926	10.84
16	1,512	620	586	2,718	4.25
17	78	27	0	105	0.16
18	0	29	36	65	0.10
19	694	269	44	1,007	1.58
20	18	0	406	424	0.66
21	3	0	0	3	0.01
22	70	0	219	289	0.45
23	30	1	2	33	0.05
24	2	0	17	19	0.03
25	0	3	3	6	0.01
26	38	40	0	78	0.12
27	12	12	1	25	0.04
28	0	2	1	3	0.01
Site C:					
June 29	0	2	3	5	0.01
30	3	7	7	17	0.03
July 1	10	10	10	30	0.05
2	0	0	3	3	0.01
3	2	2	2	0	0.01
4	0	0	0	0	0.00
Total	6,975	12,458	11,200	63,886	100.00

[1] For days where no hourly catches are given, the totals are estimated catches based on 4 days' simultaneous fishing at site A and index site.

APPENDIX TABLE 3.—*Kvichak River smolt catches, by site, day, and hour, 1957*

Site and date	2200–2300	2300–2400	2400–0100	Total [1]	Percent
Index site:					
May 28	628	454	2	1,084	4.26
29	1	8	87	96	0.38
30				69	0.27
31				9,274	36.48
June 1	2,124	3,640	344	6,108	24.02
2				178	0.70
3	175	179	245	599	2.36
4	2	0	0	2	0.01
5	991	1,447	998	3,426	13.47
6	166	303	4	473	1.86
7	0	3	0	3	0.01
8	90	0	1	91	0.36
9	0	4	0	4	0.02
10	0	1	1	2	0.01
11	229	0	2	231	0.91
12	1	0	0	1	0.00
13	1	0	1	2	0.01
14	0	0	0	0	0.00
15	0	0	1	1	0.00
16				[2] 33	0.13
17	0	60	5	65	0.26
18				73	0.29
19				292	1.15
20				49	0.19
21				186	0.73
22				216	0.85
23				[2] 140	0.55
24				[2] 140	0.55
25				[2] 140	0.55
26				[2] 140	0.55
27	0	0	65	65	0.26
28				22	0.09
29				321	1.26
30				144	0.57
Site C:					
July 1				112	0.44
2				56	0.22
3				159	0.63
4				291	1.14
5				66	0.26
6				120	0.47
7				29	0.11
8				15	0.06
9				45	0.18
10				0	0.00
11				30	0.12
12				59	0.23
13				165	0.65
14				31	0.12
15				156	0.61
16				16	0.06
17				26	0.10
18				45	0.18
19				92	0.36
20				43	0.17
21				6	0.02
22				12	0.05
23				130	0.51
24				50	0.20
Total	4,408	6,099	1,746	25,424	100.00

[1] For days where no hourly catches are given, the net was not checked at the end of each index hour.

[2] The index net was not fished; the "total" was estimated as the average of the catches on the preceding and following days.

APPENDIX TABLE 4.—*Kvichak River smolt catches at index site, by day and hour, 1958*

Date	2200–2300	2300–2400	2400–0100	Total	Percent
May 10	7	11	14	32	0.00
11	19	48	102	169	0.01
12	676	523	522	1,721	0.09
13	71	87	101	259	0.01
14	21	37	43	101	0.01
15	72	176	58	306	0.02
16	25	183	155	363	0.02
17	2	112	280	394	0.02
18	430	95	392	917	0.05
19	304	668	386	1,358	0.07
20	[1] 540	885	[1] 1,248	2,673	0.14
21	7,000	6,000	1,864	14,864	0.78
22	131,250	[1] 45,763	1,621	178,634	9.34
23	137,418	[1] 81,793	5,313	224,524	11.74
24	10	3	0	13	0.00
25	177	93	429	699	0.04
26	[1] 326,972	[1] 131,643	20,238	478,853	25.03
27	166,796	99,099	8,554	274,449	14.35
28	20,254	47,565	7,356	75,175	3.93
29	360	38	6	404	0.02
30	4,620	846	1,566	7,032	0.37
31	15,096	75,276	31,191	121,563	6.36
June 1	90	38	4	132	0.01
2	2,809	20,885	6,664	30,358	1.59
3	37,851	60,375	43,491	141,717	7.41
4	1,110	3,627	986	5,723	0.30
5	165	44	46	255	0.01
6	1,900	464	870	3,234	0.17
7	2,756	2,438	2,120	7,314	0.38
8	6,225	11,556	12,285	30,066	1.57
9	1,876	252	97	2,225	0.12
10	216	197	291	704	0.04
11	2,808	489	2,235	5,532	0.29
12	23,678	16,585	28,928	69,191	3.62
13	[1] 51,176	[1] 42,375	1,890	95,441	4.99
14	13,700	[1] 14,729	1,590	30,019	1.57
15	18,408	17,384	8,692	44,484	2.32
16	979	2,086	1,916	4,981	0.26
17	357	842	2,052	3,251	0.17
18	2,450	3,200	965	6,615	0.35
19	51	7	0	58	0.00
20	4,183	2,068	612	6,863	0.36
21	780	154	59	993	0.05
22	1,674	920	1,001	3,595	0.19
23	2,430	878	255	3,563	0.18
24	176	926	1,316	2,418	0.12
25	1,523	499	1,395	3,417	0.18
26	139	563	523	1,225	0.06
27	645	1,246	2,871	4,762	0.25
28	225	168	11	404	0.02
29	726	841	1,849	3,416	0.18
30	3,276	2,624	4,980	10,880	0.57
July 1	740	1,386	1,848	3,974	0.21
2	415	82	546	1,043	0.05
3	27	31	8	66	0.00
4	30	50	54	134	0.01
5	141	13	57	211	0.01
Total	997,855	700,966	213,946	1,912,767	100.01

[1] Partly a visual estimate of the fish passing through the net with the cod end removed.

APPENDIX TABLE 5.—*Kvichak River smolt catches at index site, by day and hour, 1959*

Date	2200 2300	2300–2400	2400–0100	Total	Percent
May 23	81	270	946	1,297	0.08
24	48	2	60	110	0.01
25	208	2,592	1,188	3,988	0.24
26	67,701	97,470	68,000	233,171	14.19
27	83,148	96,774	135,846	315,768	19.22
28	21,154	1,905	1,028	24,087	1.47
29	1,100	34,385	122,396	157,881	9.61
30	29,736	93,840	109,121	232,697	14.16
31	107,396	166,842	150,248	424,486	25.83
June 1	49,529	104,900	17,378	171,807	10.46
2	1,006	4,886	42,673	48,565	2.96
3	143	19	3	165	0.01
4	73	132	254	459	0.03
5	340	742	585	1,667	0.10
6	815	200	10	1,025	0.06
7	4,118	6,918	2,663	13,699	0.83
8	138	257	158	553	0.03
9	0	220	180	400	0.02
10	140	0	2	142	0.01
11	0	0	0	[1] 74	0.00
12	0	0	5	5	0.00
13	0	0	0	[1] 83	0.01
14	23	128	10	161	0.01
15	0	0	0	[1] 952	0.06
16	924	507	312	1,743	0.11
17	0	0	0	[1] 1,027	0.06
18	306	3	2	311	0.02
19	0	0	0	[1] 1,444	0.09
20	472	1,121	983	2,576	0.16
21	0	0	0	[1] 1,325	0.08
22	0	4	69	73	0.00
23	0	0	0	[1] 94	0.01
24	108	5	2	115	0.01
25	0	0	0	[1] 70	0.00
26	12	2	10	24	0.00
27	0	0	0	[1] 351	0.02
28	187	438	53	678	0.04
Total	368,906	614,562	654,185	1,643,073	100.00

[1] The index net was not fished: the total was estimated as the average of the catches of the preceding and following days.

APPENDIX TABLE 6.—*Kvichak River smolt catches for 12 days of 24-hour fishing, at index site, 1957*

Date	2200–0200	0200–0600	0600–1000	1000–1400	1400–1800	1800–2200	Total
May 30	103	675	[1] 35	[1] 35	4	[1] 23	875
June 1	7,056	171	0	3	0	0	7,230
3	787	99	0	0	0	0	886
5	3,477	1	0	0	0	0	3,478
6	496	[1] 20	[1] 18	0	0	0	534
7	3	0	0	0	0	0	3
12	1	0	0	0	0	5	6
13	2	0	0	0	0	0	2
14	0	0	0	0	0	1	1
22	217	3	0	0	0	0	220
29	[1] 331	[1] 19	[1] 10	[1] 10	1	31	402
July 20	24	[1] 2	[1] 1	0	0	1	28
Total	12,497	990	64	48	5	61	13,665
Percent	91.45	7.24	0.47	0.35	0.04	0.45	100.00

[1] This figure is partly an estimate made necessary because the nets were not checked exactly at 4-hour intervals.

APPENDIX TABLE 7.—*Kvichak River smolt catches for 9 days of 24-hour fishing, at index site, 1958*

Date	2200–0200	0200–0600	0600–1000	1000–1400	1400–1800	1800–2200	Total
May 13	473	796	3	1	1	0	1,274
24	15	3	107	280	179	63	647
28	78,669	10,812	2,499	510	867	322	93,679
30	9,188	4,896	4,592	105,392	15,565	16,747	156,380
31	129,429	6,235	311	415	174	316	136,880
June 1	149	11	6	1,367	493	520	2,546
2	33,084	1,642	1,071	718	4,098	15,784	56,397
3	151,356	7,797	24,200	10,467	2,490	5,493	201,803
4	5,897	1,030	469	250	3,182	2,937	13,765
Total	408,260	33,222	33,258	119,400	27,049	42,182	663,371
Percent	61.54	5.01	5.01	18.00	4.08	6.36	100.00

APPENDIX TABLE 8.—*Weighted age composition of Kvichak River salmon, at index site, 1955*

Date	Number of samples	Number of fish	Age 1	
			Percentage in samples [1]	Index catch
June 2	2	191	4.2	342
4	4	377	0.3	24
5	4	690	2.9	3,888
6	2	306	10.8	884
7	5	644	16.6	4,038
8	6	789	18.0	3,013
9	3	437	35.5	3,529
Total	26	3,434	....	15,718 (or 7.3%)

[1] Determined from daily unweighted length frequencies and scale samples.

APPENDIX TABLE 9.—*Weighted age composition of Kvichak River salmon, at index site, 1956*

Date [1]	Number of samples	Number of fish	Age 1	
			Percentage in samples [2]	Index catch
May 26	1	58	12.1	7
29	1	73	5.5	4
June 1	2	106	13.2	90
5	1	54	72.2	39
7	3	250	34.0	3,213
8	3	240	41.7	1,721
9	2	163	30.7	568
10	1	115	34.8	40
11	1	103	50.5	70
14	2	169	36.7	1,134
15	3	341	38.7	2,680
16	2	179	52.5	1,427
19	1	112	75.0	755
22	1	119	94.1	272
26	1	65	13.9	11
Total	25	2,147	....	12,031 (or 39.2%)

[1] Samples and catches from May 26 through June 5 from site A.
[2] Determined from daily unweighted length frequencies and scale samples.

APPENDIX TABLE 10.—*Weighted age composition of Kvichak River salmon, at index site, 1957*

Date	Number of samples	Number of fish	Age 1	
			Percentage in samples [1]	Index catch
May 28	1	86	54.7	593
29	1	87	37.9	36
30	2	235	92.8	64
31	3	318	83.0	7,697
June 1	2	164	48.2	2,944
2	1	90	56.7	101
3	3	268	74.6	447
5	3	377	97.6	3,344
6	1	81	38.3	181
Total	17	1,706	....	15,407 (or 72.3%)

[1] Determined from daily unweighted length frequencies and scale samples.

APPENDIX TABLE 11.—*Weighted age composition of Kvichak River salmon, at index site, 1958*

Date	Number of samples	Number of fish	Age 1	
			Percentage in samples [1]	Index catch
May 22	3	459	94.1	168,095
23	3	535	97.9	219,806
26	3	546	96.7	463,051
27	3	535	98.3	269,783
28	3	628	99.7	74,949
31	3	659	100.0	121,563
June 2	3	683	99.4	30,176
3	3	668	99.9	141,575
8	3	624	99.5	29,916
12	3	622	99.5	68,845
13	3	652	99.9	95,346
14	3	623	99.8	29,959
15	3	630	100.0	44,484
Total	39	7,864	....	1,757,548 (or 97.9%)

[1] Determined from daily unweighted length frequencies and scale samples.

APPENDIX TABLE 12.—*Weighted age composition of Kvichak River salmon, at index site, 1959*

Date	Number of samples	Number of fish	Age 1	
			Percentage in samples [1]	Index catch
May 26	3	156	1.3	3,031
27	3	166	3.0	9,473
28	1	47	2.1	506
29	3	167	4.8	7,578
30	3	182	3.3	7,679
31	3	201	1.0	4,245
June 1	3	164	5.5	9,449
2	2	121	8.3	4,031
Total	21	1,204		45,992 (or 2.9%)

[1] Determined from daily unweighted length frequencies and scale samples.

APPENDIX TABLE 13.—*Comparison of Kvichak River smolt catches, at index site and site C, 1957*

Date	Index site		Site C	
	Catch	Percent	Catch	Percent
May 28	1,084	4.75	1,160	6.08
29	96	0.42	595	3.12
30	69	0.30	79	0.41
31	9,274	40.62	8,646	45.35
June 1	6,108	26.75	1,889	9.91
2	178	0.78	111	0.58
3	599	2.62	404	2.12
5	3,426	15.00	2,705	14.19
6	473	2.07	1,061	5.57
7	3	0.01	16	0.08
8	91	0.40	156	0.82
17	65	0.28	425	2.23
18	73	0.32	183	0.96
19	292	1.28	524	2.75
20	49	0.21	92	0.48
21	186	0.81	84	0.44
22	216	0.95	60	0.31
27	65	0.28	312	1.64
28	22	0.10	124	0.65
29	321	1.41	296	1.55
30	144	0.63	142	0.74
Total and percent	22,834	99.99	19,064	99.98

APPENDIX TABLE 14.—*Comparison of Kvichak River smolt catches, at index site and site C, 1958*

Date	Index site		Site C	
	Catch	Percent	Catch	Percent
May 10	32	0.00	92	0.01
11	169	0.01	135	0.02
12	1,721	0.09	755	0.10
13	259	0.01	121	0.02
14	101	0.01	194	0.03
15	306	0.02	472	0.06
16	363	0.02	345	0.04
17	394	0.02	571	0.07
18	917	0.05	500	0.07
19	1,358	0.07	888	0.12
20	2,673	0.14	2,510	0.33
21	14,864	0.78	11,335	1.87
22	178,634	9.34	134,189	17.48
23	224,524	11.74	69,183	9.01
24	13	0.00	5	0.00
25	699	0.04	1,347	0.18
26	478,853	25.03	82,585	10.76
27	274,449	14.35	35,208	4.59
28	75,175	3.93	51,174	6.67
29	404	0.02	228	0.03
30	7,032	0.37	19,894	2.59
31	121,563	6.34	24,005	3.13
June 1	132	0.01	261	0.03
2	30,358	1.59	3,526	0.46
3	141,717	7.41	38,501	5.02
4	5,723	0.30	3,916	0.51
5	255	0.01	287	0.04
6	3,234	0.17	3,901	0.51
7	7,314	0.38	17,706	2.31
8	30,066	1.57	4,341	0.57
9	2,225	0.12	2,961	0.39
10	704	0.04	1,587	0.21
11	5,532	0.29	3,672	0.48
12	69,191	3.62	62,654	8.16
13	95,441	4.99	79,377	10.34
14	30,019	1.57	25,729	3.35
15	44,484	2.32	16,457	2.14
16	4,981	0.26	7,954	1.04
17	3,251	0.17	3,115	0.41
18	6,615	0.35	4,480	0.58
19	58	0.00	500	0.07
20	6,863	0.36	3,954	0.52
21	993	0.05	758	0.10
22	3,595	0.19	4,650	0.61
23	3,563	0.18	4,738	0.62
24	2,418	0.12	3,424	0.45
25	3,417	0.18	5,550	0.72
26	1,225	0.06	2,116	0.28
27	4,762	0.25	2,159	0.28
28	404	0.02	861	0.11
29	3,416	0.18	3,294	0.43
30	10,880	0.57	7,711	1.00
July 1	3,974	0.21	5,006	0.65
2	1,043	0.05	2,556	0.33
3	66	0.00	309	0.04
4	134	0.01	438	0.06
5	211	0.01	136	0.02
Total and percent	1,912,767	99.99	767,321	100.02

APPENDIX TABLE 15.—*Weighted age composition of Kvichak River salmon, at site C, 1957*

Date	Number of samples	Number of fish	Age 1	
			Percentage in samples [1]	Site C catch
May 28	1	94	74.5	864
29	1	74	36.5	217
30	1	85	57.6	46
31	2	164	56.1	4,850
June 1	3	294	69.0	1,303
2	None	None	[2] 75.4	84
3	1	121	81.8	330
5	2	223	96.9	2,621
6	1	161	88.8	942
Total	12	1,216	...	11,257 (or 67.6%)

[1] Determined from daily unweighted length frequencies and scale samples.

[2] Calculated as the average of June 1 and 3.

APPENDIX TABLE 16.—*Weighted age composition of Kvichak River salmon, at site C, 1958*

Date	Number of samples	Number of fish	Age 1	
			Percentage in samples [1]	Site C catch
May 22	2	310	96.1	128,956
23	3	462	99.1	68,560
26	2	392	99.0	81,759
27	2	362	99.2	31,950
28	3	623	99.7	51,020
31	3	624	99.8	23,957
June 2	3	677	100.0	3,526
3	3	684	99.9	38,462
8	3	636	99.5	4,319
12	3	619	99.8	62,529
13	3	634	99.8	79,218
14	3	627	99.8	25,678
15	3	607	100.0	16,457
Total	36	7,257	...	616,391 (or 98.3%)

[1] Determined from daily unweighted length frequencies and scale samples.

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EARLY DEVELOPMENTAL STAGES OF PINK SHRIMP, *PENAEUS DUORARUM* FROM FLORIDA WATERS

By SHELDON DOBKIN

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ABSTRACT

The eggs and the larval and first two postlarval stages of the pink shrimp, *Penaeus duorarum* Burkenroad, from Florida waters are described and illustrated. A series of drawings of the rostra of advanced postlarvae is included.

The first six larval stages through the first protozoea were reared from eggs spawned in the laboratory. The remaining larval and postlarval stages are described from specimens obtained in plankton samples taken in the Florida Bay and Dry Tortugas areas.

The larval and postlarval stages of *P. duorarum* are compared with those of *P. setiferus*. Postlarval stages of *P. aztecus* are compared with those of *P. duorarum*.

EARLY DEVELOPMENTAL STAGES OF PINK SHRIMP, *PENAEUS DUORARUM*, FROM FLORIDA WATERS

By SHELDON DOBKIN, MARINE LABORATORY
UNIVERSITY OF MIAMI

Study of the life history of penaeid shrimps has received great impetus in the past 25 years with the increased commercial importance of many of the species. The species of most importance commercially belong to the genus *Penaeus* and the developmental stages of several members of this genus have been described.

Three species of *Penaeus* are fished commercially along the South Atlantic and Gulf coasts of the United States. Of these, *P. setiferus* has received the most study; its early life history has been described by Pearson (1939). The larval development of *P. duorarum* and *P. aztecus* has not been described; however, some information on the postlarval and juvenile phases of their life history is available (Williams, 1953, 1955, 1959).

The pink shrimp, *P. duorarum*, supports a valuable fishery in Florida and accounts for approximately three-quarters of the shrimp landed in the State. The object of this study was to provide detailed descriptions of the egg and larval stages of this shrimp.

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METHODS AND MATERIALS

PLANKTON COLLECTIONS

To obtain the eggs and larvae of penaeid shrimps, which are planktonic, more than 500 plankton samples were taken between January and December, 1959, in Florida Bay and in the Dry Tortugas areas and adjacent waters. These collections were made from research vessels of the University of Miami Marine Laboratory and from commercial trawlers. Tows were made at all times of day and night and at several water depths (see table 1). The depth at which the nets were fished was determined by applying the wire angle measured by an inclinometer to the known amount of wire out. Three-quarter meter (mouth diameter) "Discovery"-type nets were used in most instances with either a No. 10 mesh silk bolting or a No. 2 mesh nylon cod end. A 1-foot (mouth diameter) "Turtox" net of No. 6 mesh silk bolting cloth was also used.

Plankton tows were generally of 30 minutes' duration except when other considerations, such as the necessity for making hydrographic observations, caused the net to be brought up sooner. A towing speed of approximately 3½ knots was maintained in most cases. The plankton was preserved in 3-percent formalin buffered with hexamethylenamine and stored in 16-ounce jars.

REARING EXPERIMENTS

Four rearing experiments were conducted from late March through July 1959. In these experiments, large females (approximately 120 to 170 mm. total length) with opaque ova were removed from the regular commercial hauls of a shrimp trawler on the Dry Tortugas fishing grounds and taken to the laboratory. The shrimp were kept

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TABLE 1.—*Station data for 161 larvae and postlarvae of* Penaeus duorarum *taken from the plankton, 1959*

Station	Date	Time	Location	Depth (m.)	Number and stage of specimens
ELH 79	Mar. 14	0510	25°39′ N., 81°41′ W.	6	2 (second postlarvae).
ELH 104	June 2	0315	24°50′ N., 82°11′ W.	0	22 (first, second, and third postlarvae).
ELH 111	3	0040	24°56′ N., 82°27′ W.	0	1 (second mysis).
ELH 112	3	0205	24°58′ N., 82°31′ W.	30	1 (first mysis).
ELH 169	July 16	2045	24°55′ N., 82°03′ W.	0	46 (all stages from first protozoea through third postlarva).
ELH 172	16	0320	24°50′ N., 82°17′ W.	0	1 (first mysis).
ELH 175	17	2152	24°51′ N., 82°09′ W.	0	4 (third protozoea and first mysis).
ELH 179	18	0150	24°54′ N., 82°05′ W.	0	1 (third mysis).
ELH 185[1]	18	0940	24°35′ N., 82°09′ W.	2	4 (advanced postlarvae).
ELH 197	18	2125	25°05′ N., 82°08′ W.	0	1 (third mysis).
ELH 221	Sept. 10	0025	24°43′ N., 82°36′ W.	28	4 (first and second protozoea).
ELH 229	10	0905	24°43′ N., 82°36′ W.	28	2 (second and third protozoea).
ELH 233	10	1300	24°43′ N., 82°36′ W.	28	25 (all stages from first protozoea through third mysis).
ELH 240	10	2105	24°43′ N., 82°36′ W.	0	18 (first and second mysis).
ELH 283	Oct. 5	2100	25°10′ N., 82°14′ W.	0	1 (second mysis).
ELH 317	10	0345	24°43′ N., 82°35′ W.	0	1 (advanced postlarva).
ELH 334a	Nov. 3	1830	Flamingo Canal	0	27 (advanced post larvae).

[1] One-minute trawl with seine.

alive in transit in plastic 20-gallon trash cans containing sea water circulated by a 12-volt pump. About 1 dozen shrimp were held successfully in each container for the duration of the 160-mile trip. The water was changed midway of the trip.

At the laboratory three to six shrimp were placed in 15-gallon aquariums, and circulation was maintained by filtering sea water through No. 6 silk bolting cloth (fig. 1). The small size of the apertures (0.24 mm.) made it certain that all eggs found in an aquarium were spawned by the shrimp being held. The runoff from each tank was drained through a section of plankton netting fitted to a collecting jar. During the course of each experiment the collecting jars and aquariums were examined for eggs and larvae, which were removed and studied microscopically. Periodically, each tank was drained and its entire contents examined.

Eggs and nauplii removed from the aquariums were held in a variety of containers ranging from petri dishes to a 4-gallon bell jar. The sea water in the smaller containers was changed frequently. In the larger vessels it was generally not renewed during the course of an experiment, but in several instances was aerated by means of an air pump. On one occasion a glass plunger provided mechanical agitation of the water in the bell jar.

Several types of food were introduced into the containers when the larvae in them reached the first protozoeal stage. The first of these was "Liquifry," a food intended for fish fry and made up of particles the size of ciliate protozoans. In subsequent experiments, cultures of the unicellular green algae, *Chlamydomonas* sp. and *Dunaliella* sp., were fed to the larvae.

In the last two experiments, an attempt was made to minimize bacterial contamination by adding antibiotics to the water in which larvae were being held. In one instance, approximately 400,000 units of penicillin were added to each of several of the gallon jars; in another, several milliliters of a broad-spectrum antibiotic (10 milligrams/milliliter aureomycin, 2 mg./ml. chloramphenicol, 2 mg./ml. streptomycin) were used.

First Experiment

The first rearing experiment took place from March 26 to April 2. Six ripe female shrimp were brought to the laboratory on March 30; three shrimp were placed in a 15-gallon aquarium, and the other three in a large concrete holding tank. Eggs were found in the collecting jar of the aquarium the following morning, and the entire aquarium was drained and the eggs gathered. The eggs were placed in a variety of containers (in 32-, 16-, and 10-ounce jars and in petri dishes) and by early afternoon they were beginning to hatch. The water in which the larvae were held was changed approximately twice daily. Within 2 days the larvae that had not succumbed in the nauplius stage, approximately 10 in number, had developed to the first protozoea. They were fed on Liquifry, approximately 1 milliliter being added per 32 ounces of water, and examination of the gut of the protozoea showed that feeding had taken place. Despite this, all the remaining larvae died in the first protozoeal stage within 5 days of the time the eggs were found. Because the number of eggs spawned was relatively small and

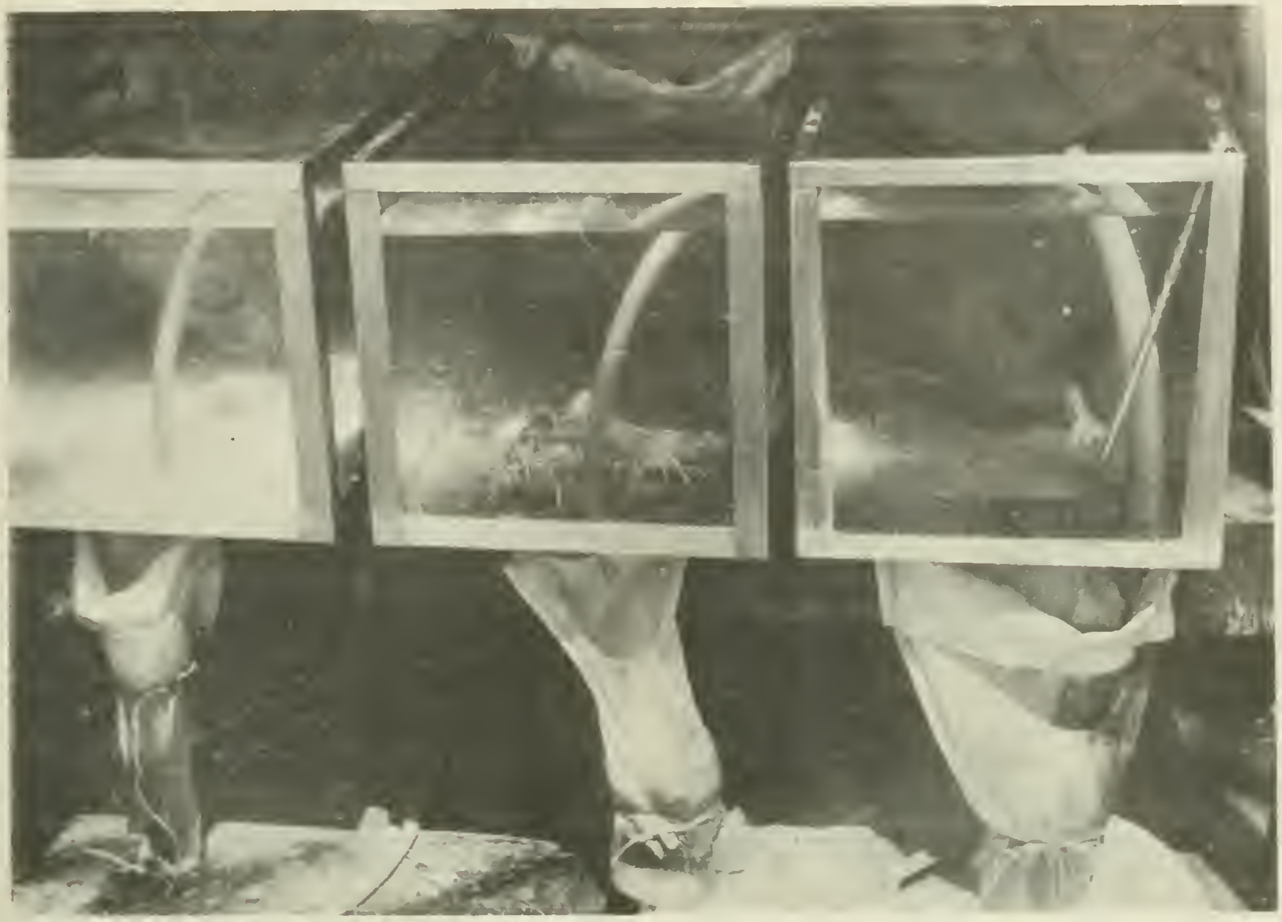

FIGURE 1.—Aquariums used in rearing experiments, showing plankton netting attached to collecting jar to catch larvae and eggs in runoff.

mortality was high, insufficient larvae were obtained to be certain of the number of naupliial stages.

Second Experiment

In the second rearing experiment, April 8 to 17, 17 shrimp were brought to the laboratory and divided among 3 aquariums. On the morning of April 13, viable eggs and both newly hatched and advanced nauplii were observed in the runoff from one aquarium. This aquarium was drained and the eggs and larvae collected and placed in 16- and 32-ounce jars as well as in a 5-gallon aquarium, the bottom of which was covered with sand and equipped with a subsand filter. Individual eggs were isolated in petri dishes in an attempt to determine the number of molts undergone by the nauplii and the interval between molts. The developing eggs and nauplii were observed continuously for 36 hours, in order to preserve specimens of each developmental stage.

The eggs isolated in petri dishes failed to develop past the first nauplius. The larvae in the 5-gallon aquarium did not survive the molt into the first protozoeal stage. Of the approximately 40 first protozoea that did develop in the 16- and 32-ounce jars, only 1 larva passed through the next molt. This high mortality in the first protozoeal stage was probably due to a combination of factors, one of which was that the larva must now seek food for the first time, having been supplied by its own yolk in the naupliial stages (Pearson, 1939; Hudinaga, 1942). During the experiment a culture of *Chlamydomonas* sp. was fed to the first protozoea in the 16- and 32-ounce jars by adding approximately one medicine dropper full of the culture per 32 ounces of water per day, and although the digestive tracts of many of the larvae were colored green, this food appeared to be inadequate. Another factor that caused high mortality was entanglement of the setae of the larvae by algae, by the shrimp's own excrement, which is emitted in long strands, and by other particles that are found in the water. The larvae so entangled settled to the bottom where they could not feed.

Eggs, the five nauplial stages, and the first protozoea were preserved in sufficient quantity during this experiment to describe these stages.

Third Experiment

The third rearing experiment took place from June 3 to June 6. Twenty-two shrimp were brought to the laboratory on June 3, and were placed in three 15-gallon aquariums. Eggs were found in two of the aquariums on the morning of June 6 and were removed and placed in 12 1-gallon jars. Approximately 400,000 units of penicillin were added to six of these jars, and the water in one was agitated mechanically. A number of the eggs developed, and two newly hatched nauplii were seen. Several hours later, however, eggs removed from the jars were not viable, and no additional nauplii were found.

Fourth Experiment

In the fourth rearing experiment, July 20–27, approximately 20 female shrimp were placed in three 15-gallon aquariums at the laboratory in the early afternoon of July 20. The following morning eggs and newly hatched nauplii were found in each aquarium and were removed to six 1-gallon jars and a 4-gallon bell jar. Approximately 5 milliliters of the broad-spectrum antibiotic were added to three of the 1-gallon jars and about 20 milliliters were added to the bell jar. The latter was agitated mechanically by a glass plunger. The water was not changed in these containers during the course of this experiment.

The larvae had advanced to the fifth nauplial stage by the late afternoon of July 22, and the following morning all the jars were found to contain first protozoea. They were fed a culture of *Dunaliella* sp. (which was used as food for oyster and clam larvae by Davis and Guillard, 1958), by adding approximately 4 milliliters to each 1-gallon jar and 10 milliliters to the bell jar daily.

High mortality again occurred in the first protozoeal stage. The larvae held in the jars to which no antibiotic was added were all dead by the afternoon of July 24, and by the morning of July 27 all of the larvae in the other jars had died. None of the larvae molted into the second protozoea despite the fact that feeding had taken place.

During this experiment, photomicrographs of the egg in various stages of development and of the nauplial and first protozoeal stages were taken.

Conclusions

To rear *Penaeus duorarum* successfully, suitable food and the prevention of crowding of the larvae are necessary. Hudinaga (1942) was successful in raising larvae of *Penaeus japonicus* through the critical protozoeal stage by feeding them the diatom *Skeletonema costatum*. He reported that the mysis stage could be raised on that diatom alone, although good results were obtained by mixing the nauplius of *P. japonicus* with the diatoms. Heldt (1938) found that the protozoea of several species of penaeids prospered on small copepods if the individual larva was isolated and the debris and excrement removed from the water.

Broad (1957) reported that caridean larvae fed on algae did no better than those that were not fed. He reared larvae to the young adult stage by feeding them *Artemia* nauplii, and limited the number of larvae placed in each 4-inch finger bowl to 10. Costlow and Bookhout (1959) were successful in rearing zoeae of the blue crab, *Callinectes sapidus*, by placing them in plastic compartmented boxes with one zoea per compartment and feeding them *Arbacia* eggs and *Artemia* nauplii. The author (unpublished data) succeeded in rearing the larvae of several species of carideans by placing from 1 to 10 larvae in each compartment of plastic compartmented boxes and feeding them on *Artemia* nauplii. Each compartment contained from 50 to 75 ml. of sea water, and the water was changed each morning.

EGG AND LARVAL STAGES

ABBREVIATIONS USED IN ILLUSTRATIONS

a1—first antenna
a2—second antenna
ab—abdomen
c—carapace
ch—chela
dt—digestive tract
e—eye
en—endopod
ex—exopod
fr—frontal organs
fu—furca
gp—gill plate
la—labium
lm—labrum
md—mandible
mp—mastigobranchial plate
mx1—first maxilla
mx2—second maxilla
mxp1—first maxilliped
mxp2—second maxilliped
mxp3—third maxilliped
o—ocellus
ped—peduncle
per—pereiopods
pl—pleopods
pr—protopod
r—rostrum
sc—scaphognathite
st—statocyst
su—supraorbital spine
th—thorax
u—uropods

EGG

Several hundred eggs were obtained from the spawning of mature female pink shrimp in the laboratory. Fifty-three viable eggs measured from 0.31 to 0.33 millimeters in diameter. The viable eggs are yellow brown in color and opaque, although when light is reflected in a certain way, the chorion shows the blue hue reported by Pearson (1939) for the eggs of *P. setiferus.*

The complete development of the fertilized egg was not observed, since the eggs were already in an advanced state when found. The development of eggs of *Penaeus japonicus* is adequately described by Hudinaga as summarized by Pearson (1939). Development in *P. duorarum* may be similar, since conditions under which the eggs of the two species of shrimp were reared and development subsequent to hatching are comparable. Photomicrographs of several stages of viable eggs were made (fig. 2).

Hatching was observed by the author in the laboratory. At water temperatures of 27° to 29° C., the nauplius emerges about 13 or 14 hours after the eggs are spawned (Hudinaga, 1942). Prior to its emergence, the nauplius moves its appendages convulsively at short intervals. After the furcal spines puncture the egg membrane, the nauplius emerges, posterior half first, by pushing against the membrane with the first antennae. Emergence from the egg requires 2 to 3 minutes.

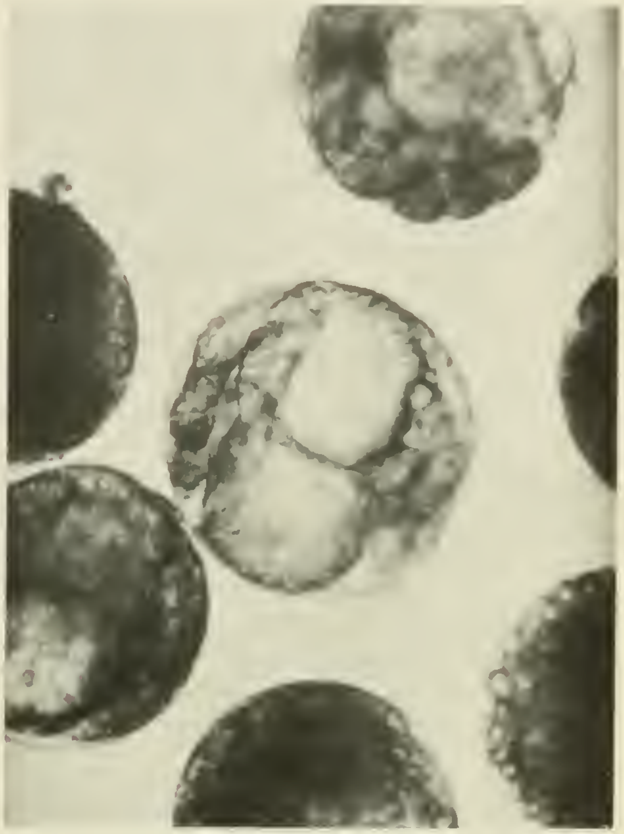

FIGURE 2.—Photomicrograph of eggs in several stages of development.

FIRST NAUPLIUS

Individuals of the first naupliar stage (fig. 3) ranged from 0.35 to 0.40 mm. in body length. Their greatest body width was from 0.18 to 0.20 mm. Body length was measured from the anterior to the posterior end exclusive of the furcal spines. Greatest body width between the lateral margins was measured dorsally and occurred at a point between the first two pairs of appendages. Description of the first nauplius is based on 13 specimens raised from eggs.

The nauplius is yellow brown in color and opaque, the opaqueness being more pronounced in preserved specimens. Viewed dorsally the body is pear-shaped, the anterior part being the wider.

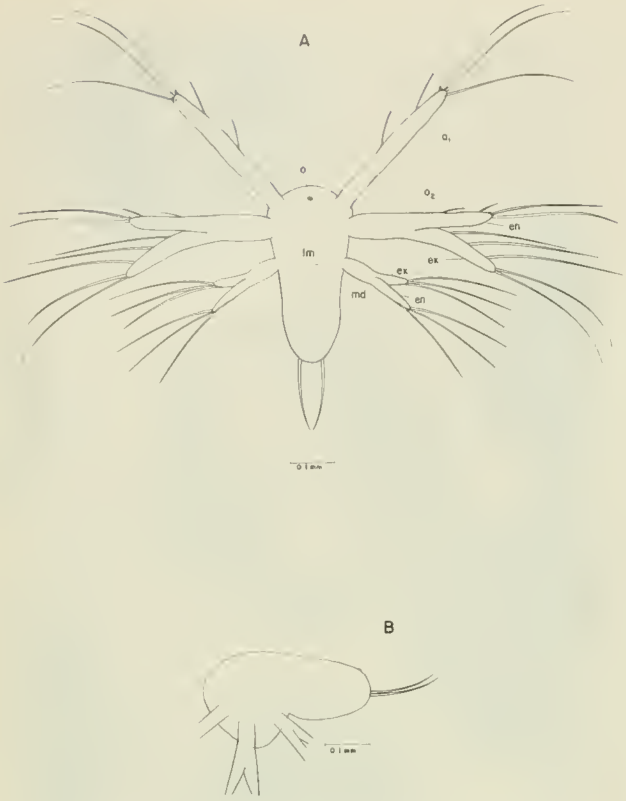

FIGURE 3.—First nauplius. (A) Ventral view. (B) Lateral view.

Newly hatched first nauplii resemble two spheres joined at the middle (fig. 4), but shortly thereafter they completely unfold and become typically pyriform (fig. 5).

Viewed laterally, the anterior part is elliptical, due to development of the labrum (fig. 3B). This structure is present at the point where the anterior and posterior halves join and where the posterior half is flexed ventrally. The body appears to be divided into anterior and posterior parts with a constriction between; nevertheless, it is not truly segmented.

An ocellus, or "nauplial eye," is present near the anterior end of the body. Posteriorly, there is a dorsally flexed pair of furcal spines which are approximately two-fifths as long as the body. A small dorsomedian triangle-shaped spine (fig. 3B) is present near the posterior end of the body.

Three pairs of appendages, natatory in function, are present: first antennae, second antennae, and mandibles. The antennae are considerably larger than the mandibles.

The first antenna is uniramous and finger-shaped and is slightly more than three-quarters the length of the body. It bears 2 short lateral setae, 2 long terminal setae, and a third long seta which appears to be terminal, but which actually arises from the dorsal surface of the appendage. The bud of a third terminal seta is present. "Short" setae measure less than 0.1 mm. in length, "moderate" setae between 0.1 and 0.2 mm., and "long" setae more than 0.2 mm.

The second antenna is biramous, the exopod slightly longer than the endopod and equal in length to the first antenna. The endopod bears 2 short lateral and 2 long terminal setae. The bud of a third terminal seta is present. The exopod bears 3 long lateral and 2 long terminal setae.

The mandible is biramous and approximately half the length of the first appendage. Each ramus bears 3 long setae. All setae on the exopod are terminal. Two of the setae on the endopod are terminal, the third seta arises from a constriction in the appendage approximately four-

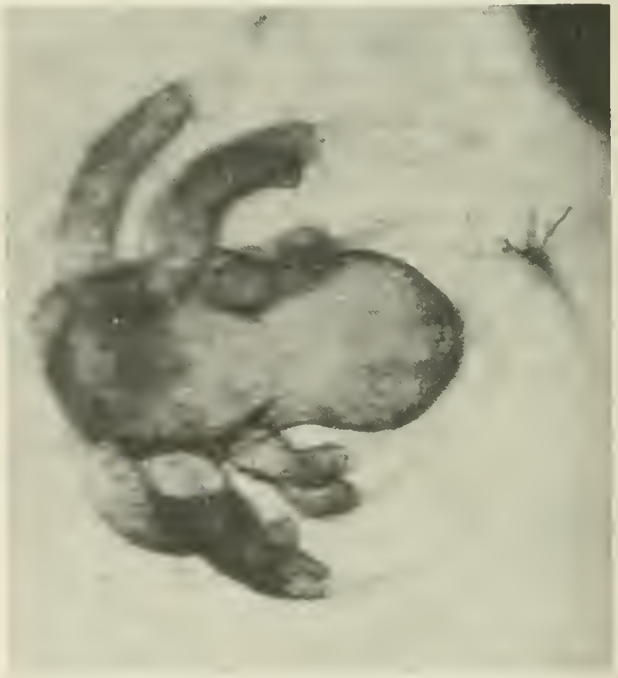

FIGURE 4.—Photomicrograph of first nauplius immediately following hatching.

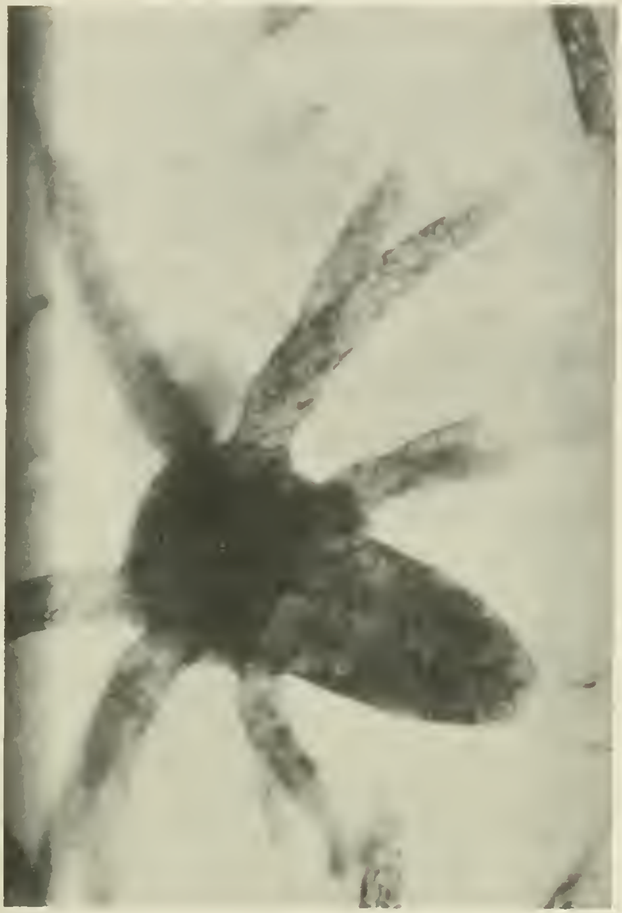

FIGURE 5.—Photomicrograph of first nauplius soon after hatching.

fifths of the distance from the body. Although setation of the first and the second appendage varies in the different nauplial stages, that of the mandibles remains constant

During the nauplial stages, the larvae feed on yolk granules, which, because of their opaqueness, can easily be seen in the transparent body of the nauplius. The description of locomotion in the nauplius of *P. setiferus* (Pearson, 1939) and *P. japonicus* (Hudinaga, 1942) was found to hold true for *P. duorarum*. The nauplius swims upward by a rapid beating of its appendages, which lasts approximately 5 seconds; after that the nauplius sinks dorsal side down with its appendages extending upwards. This period of inactivity lasts several times longer than the period of activity, being from 15 to 30 seconds in duration.

SECOND NAUPLIUS

Specimens of the second nauplius (fig. 6) measured 0.40 to 0.45 mm. in length and 0.18 to 0.20 mm. in body width. The major differences between this stage and the preceding one are in the setation of the first and second antennae, the appearance of setules on the longer setae, and a slight change in the shape of the body. The description of the second nauplius is based on 27 specimens raised from eggs.

The single pair of furcal spines found in the first nauplius is still present, and no others have been added. The dorsomedian spine near the posterior end of the body is no longer present.

The first antenna bears 3 lateral setae, 2 of which are short and 1 is of moderate length; also 3 terminal setae, 1 of which is long, 1 moderate, and 1 short.

A short terminal seta has replaced the bud present in the preceding stage on the endopod of the second antenna. A short terminal seta is also added to the exopod of this appendage, making a total of 3 lateral and 3 terminal setae. The number of setae on the exopod of the second antenna increases by 1 in each successive nauplial stage and the setation of this appendage is therefore an excellent characteristic for differentiating between the various stages.

The endopod and exopod of the mandible continue to bear 3 long setae each, in the same position as in the preceding stage.

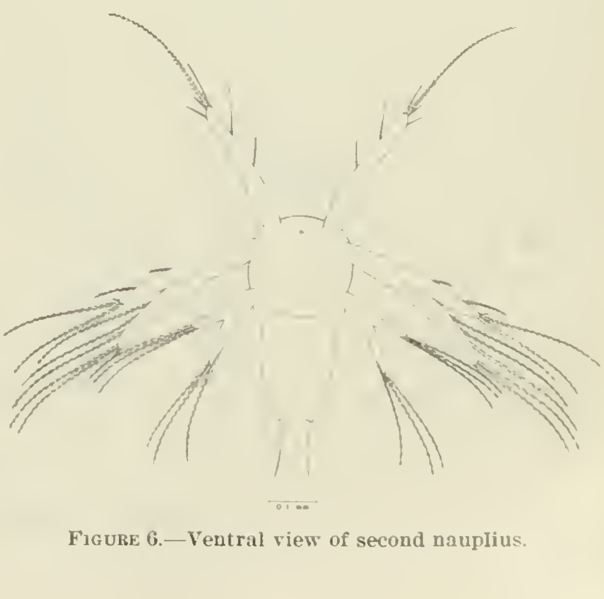

FIGURE 6.—Ventral view of second nauplius.

The posterior portion of the body of the second nauplius has become somewhat elongated. The caudal end is now truncate or concave rather than rounded.

The longer setae of the appendages have become plumose in the second nauplius with the addition of fine setules. The appendages remain unsegmented. The furcal spines do not acquire the distinct barbs reported by Hudinaga (1942) for *P. japonicus*, but their margins are no longer smooth.

THIRD NAUPLIUS

Specimens of the third nauplial stage (fig. 7) ranged in length from 0.45 to 0.49 mm. and from 0.17 to 0.20 mm. in greatest body width. Measurements were made on 24 specimens raised from eggs. The major differences between this and the preceding stage are the development of 2 distinct furcal processes, the addition of 2 spines on each of these, and differences in the setation and the first sign of segmentation of the appendages.

The caudal end of the body is now divided into 2 furcal processes with a distinct notch between. Each furca bears 3 spines, the middle one being approximately two-fifths the length of the body. The external spine measures about one-third the length of the median one and the internal spine about one-sixth. The median spine bears minute barbs but the other 2 spines are smooth. The furcal spines are flexed dorsally, as can be seen in lateral view.

The first antenna has lost its posterolateral seta and now bears 2 lateral and 3 terminal setae. The basal portion of this appendage shows traces of the segmentation that will appear in the next molt.

The endopod of the second antenna has the same complement of setae as in the preceding stage; however, the anteriormost of the terminal setae has grown to almost the length of the others.

The exopod of the second antenna has added another terminal seta, making a total of 3 lateral and 4 terminal setae.

The setation of the mandible remains the same.

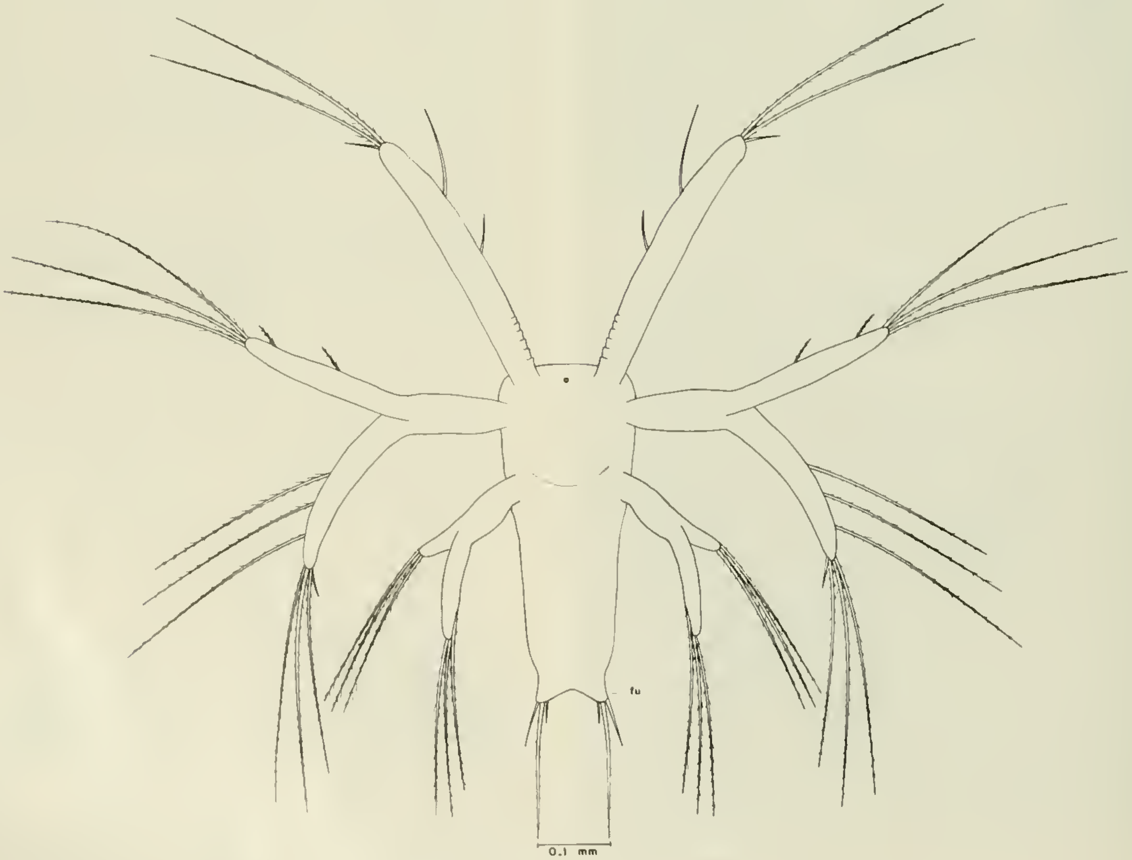

FIGURE 7.—Ventral view of third nauplius.

FOURTH NAUPLIUS

The fourth nauplii (fig. 8) examined measured from 0.48 to 0.55 mm. in body length and from 0.18 to 0.20 mm. in greatest body width. Six specimens that had been reared from eggs were studied. The major differences between this and the preceding stage are in the number of furcal spines, the appearance of the next four pairs of appendages, and segmentation and setation of the appendages.

There are now 5 spines on each furcal process, with the addition of 2 weak spines external to the 3 already present in the preceding stage. The longest spine bears minute barbs, while the other 4 are smooth.

This stage is the first in which there is a definite segmentation of the appendages. This segmentation is often indistinct and the best criterion for its determination is the presence of indentations along the margins of the appendages.

The frontal organs reported to be present in late nauplial stages in several other species of penaeids were never seen in this stage in *P. duorarum*, although several specimens were examined under 500 power specifically for this character.

FIFTH NAUPLIUS

Individuals of the fifth nauplial stage (figs. 9 and 10) measured from 0.53 to 0.61 mm. in body length and from 0.17 to 0.20 mm. in greatest body width, based on 28 specimens raised from eggs. The most noticeable differences between this and the preceding stage are the development of the masticatory portion of the mandible, the transparency of the endopod of that appendage, the increased number of furcal spines, the outline of a future carapace, and the setation of the appendages.

The furcal processes now bear 7 spines each, with the addition of 2 spines, 1 weak and 1 moderate, internal to the 5 found on each furca in the preceding stage. The 3 median spines bear minute barbs.

Frontal organs were observed on the anterior margin of several fifth nauplii taken from the

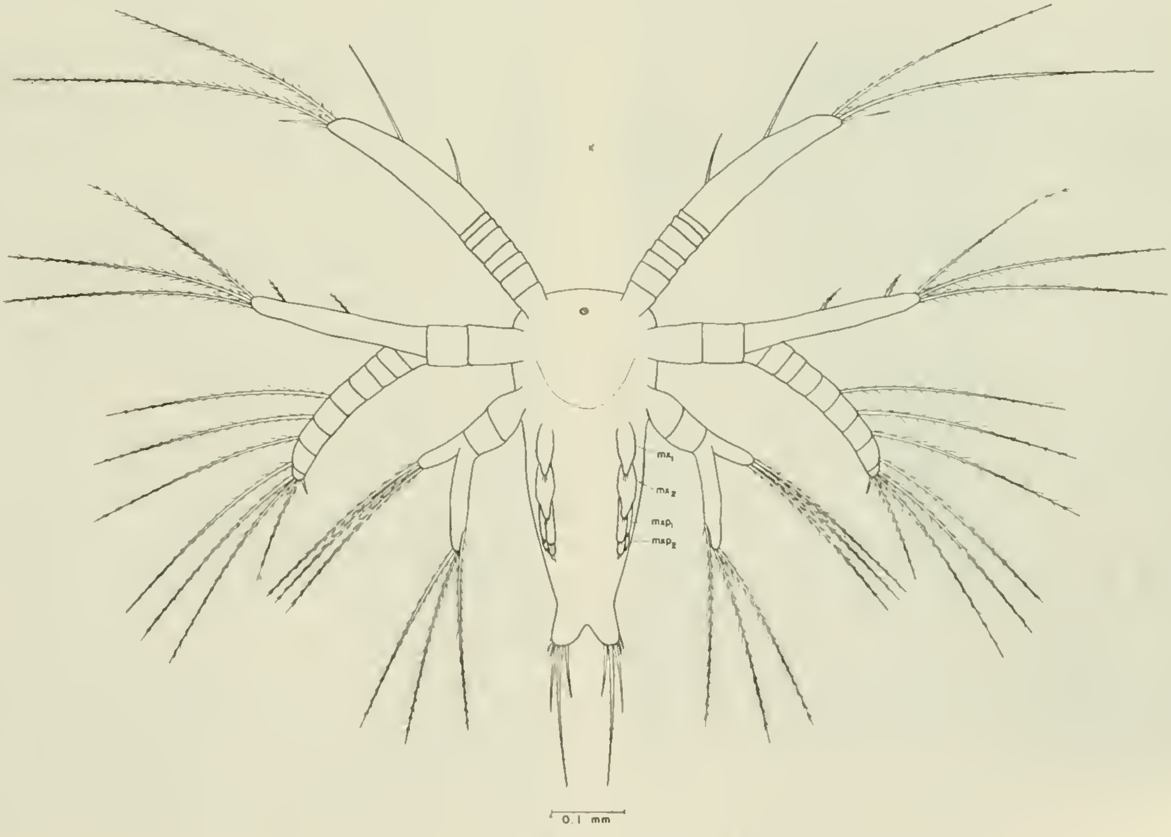

FIGURE 8.—Ventral view of fourth nauplius.

plankton. The original examination of material obtained from rearing experiments did not disclose these structures, but a photomicrograph (fig. 9) shows them clearly. With this proof of their existence and their subsequent discovery on the planktonic specimens, the presence of frontal organs was established.

The first antenna now bears 3 setae on the anterolateral and 2 on the posterolateral surfaces, as well as 3 terminal setae. This is a total of 8 setae as compared with the 5 found on this appendage in the preceding stage. The segmentation remains the same as in the fourth nauplius.

The endopod of the second antenna is unsegmented and bears 3 lateral and 4 terminal setae. Two of the lateral setae originate from the same point close to the distal end of the endopod. The exopod of the appendage now bears 9 setae, with the addition of a short lateral seta which is the most proximal to the body.

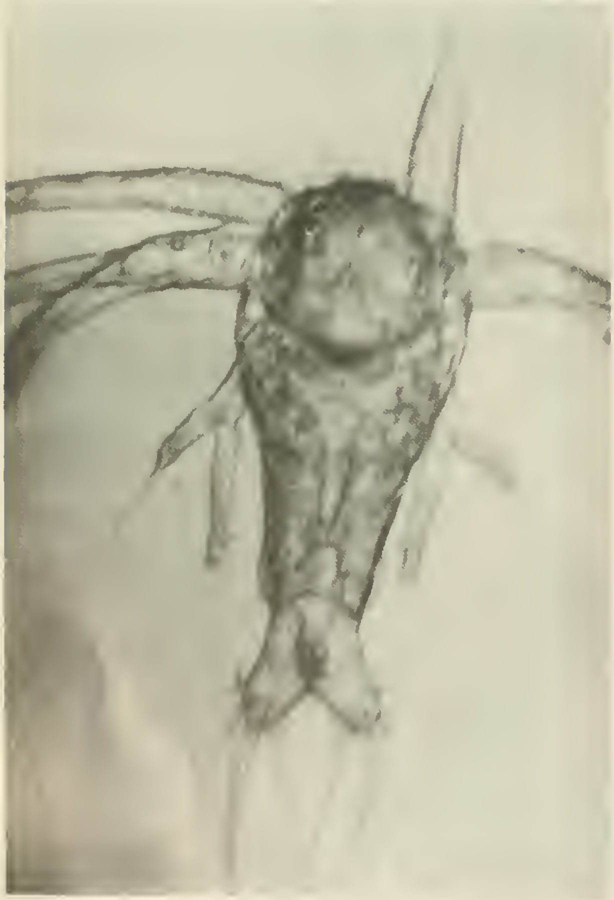

Figure 9.—Photomicrograph of fifth nauplius. (Note frontal organs.)

The basal portion of the protopod of the mandible has become swollen and knoblike and bears a ring of toothlike structures. The endopod has become transparent in some specimens due to loss of its musculature. The setation is the same as in previous stages.

The maxillae and maxillipeds are further developed, and cover the major portion of the ventral surface of the body posterior to the labrum. They remain nonfunctional. The developing maxillae and maxillipeds are biramous. The exopods of the maxillae take the form of swollen knobs protruding from the distal portions of the protopods and have been termed scaphognathites. The exopods of the maxillipeds are palplike in form.

In dorsal view the body appears to be in two segments. This is due to the outline of the posterior edge of the developing carapace, which can be seen under the cuticle at about the midpoint of the body.

FIRST PROTOZOEA

Forty-two first protozoea (figs. 11 and 12) of *P. duorarum* raised from eggs measured from 0.86 to 1.02 mm. in body length, from 0.35 to 0.44 mm. in body width at the widest part of the carapace, and from 0.40 to 0.49 mm. in carapace length. Seven first protozoea taken from the plankton measured from 0.98 to 1.14 mm. in body length.

The first protozoea represents the most radical change in the form of the larva up to this point. The body is clearly divided into two parts. The anterior part is covered by the carapace, which is just under one-half the body length. The carapace is rounded anteriorly with a notch at the midline. The posterior edge of the carapace is nearly straight and covers the basal portion of the second maxillipeds. The narrower posterior part is divided into a thorax of six segments and an unsegmented abdomen. The junction of thorax and abdomen is marked by a slight swelling in the latter.

Another feature differentiating this stage from the preceding one is the development of compound eyes. These can be seen under the carapace, but do not become stalked until the next stage. A 2-lobed labium just posterior and dorsal to the labrum and a digestive tract are other structures

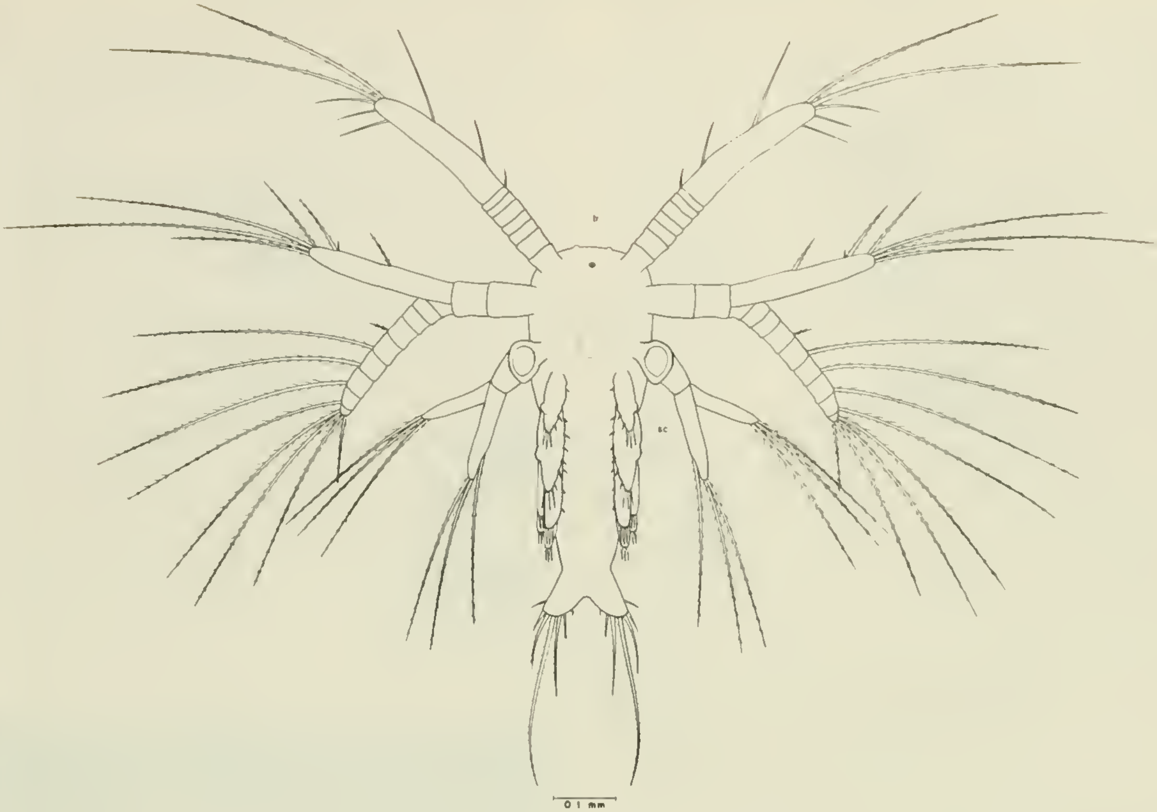

FIGURE 10.—Ventral view of fifth nauplius.

distinguishable in this stage. In addition, the mandible has lost its endopod and all but a small portion of its exopod. Its masticatory surface has, however, developed considerably. During this stage the larvae cease living on yolk and begin to seek nourishment in the water.

The ocellus persists in the midline between the developing compound eyes. Just posterior to the ocellus the two large lobes of the liver, which is dorsal to the mouth, can be seen in ventral aspect. The labrum is conspicuous as a roughly oval structure located ventrally in about the middle of the area covered by the carapace. Its posterior or free edge has a slight notch at the midline which is provided with short bristles, and the anterior edge is marked by a well-developed spine. The two lobes of the labium extend from under the labrum and have bristles along their median borders. The greater portion of the mandible consists of an irregularly shaped median masticatory lobe, which bears 6 to 8 small teeth and 3 or 4 larger ones, and a lateral rounded lobe, which bears a trace of the exopod.

The caudal furcae each bear 7 spines, as in the preceding stage. The spines have setules, except for the most external spine which is smooth. This external spine originates from the dorsal surface rather than from the lateral, terminal, or median surfaces of the furca, as do the other spines.

The first antenna is divided into three major parts. The basal portion bears 2 setae along its anterior margin. The middle portion bears 1 long seta on its anterior margin. The distal portion bears 1 dorsal and 3 terminal setae and, in addition, 1 short seta on its posterolateral margin. This is a total of 8 setae on the first antenna.

The protopod of the second antenna is 3-segmented and bears no setae. The endopod has 2 segments, the basal segment bearing 2 setae. Two additional setae are present at the junction of the 2 segments of the endopod. The distal segment bears 5 setae, making a total of 9 setae for this ramus. The exopod of the second antenna is divided into about 10 segments and bears 7 setae on its anterolateral and 2 on its posterolateral margins, as well as 4 terminal setae.

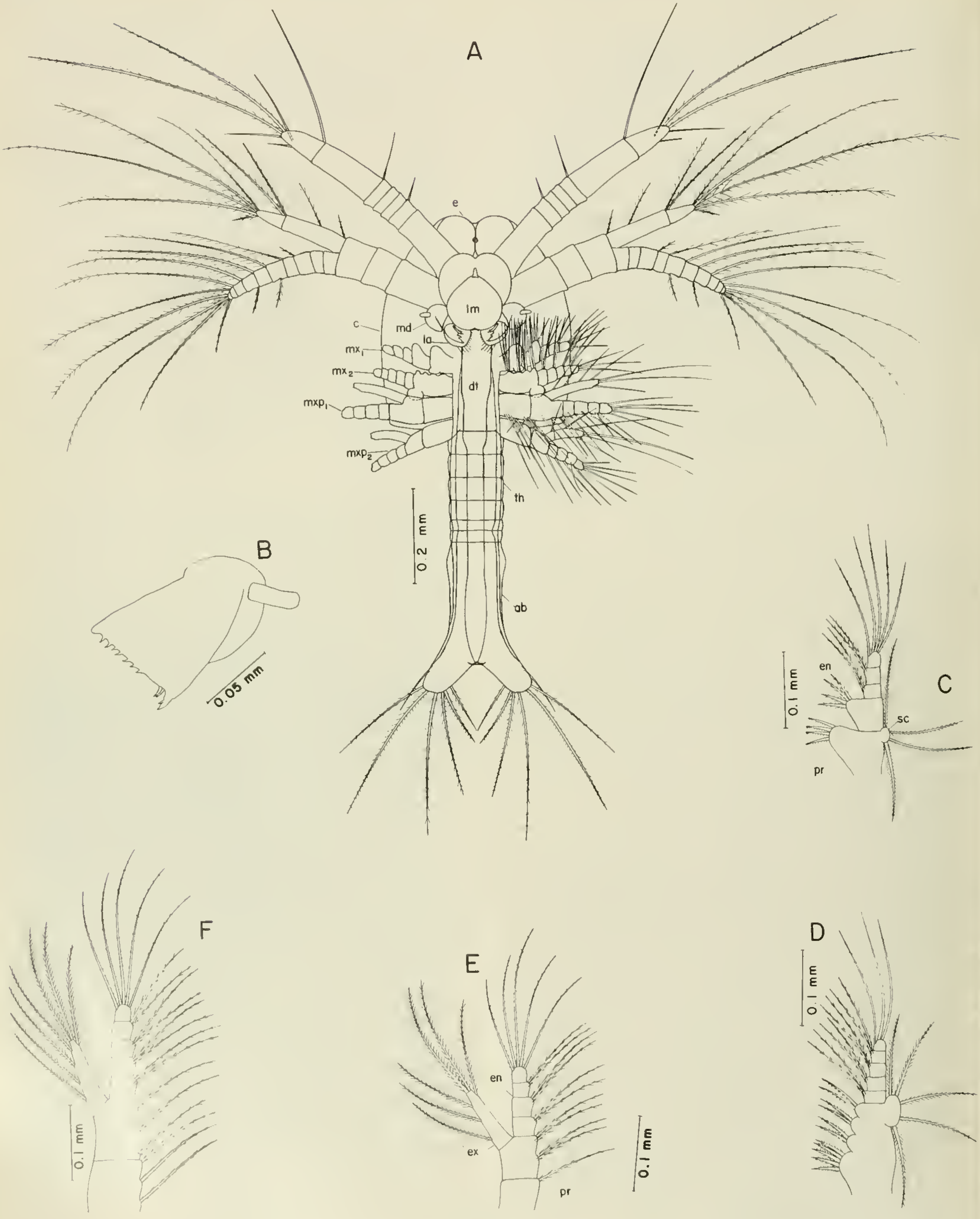

FIGURE 11.—First protozoea. (A) Ventral view. (B) Mandible. (C) First maxilla. (D) Second maxilla. (E) Second maxilliped. (F) First maxilliped.

The mandible has lost its endopod and all but a trace of its exopod, has a well-developed masticatory surface, and lies dorsal and posterior to the labrum.

The first and second maxillae and first and second maxillipeds are well developed and become functional in this stage.

The first maxilla consists of a protopod of 2 segments, an endopod of 3 segments, and a budlike exopod or scaphognathite. The inner margins of the segments of the protopod and the endopod are lobed and bear setae. The 2 segments of the protopod bear about 4 setae each. The basal and median segments of the endopod bear 2 setae each, and the terminal segment bears 5. The exopod, or scaphognathite, bears 4 setae. The 5 terminal setae of the endopod are present throughout the protozoeal and first two mysis stages. The 4 setae of the scaphognathite are present in the protozoeal and first mysis stages; the scaphognathite is not present beyond the first mysis.

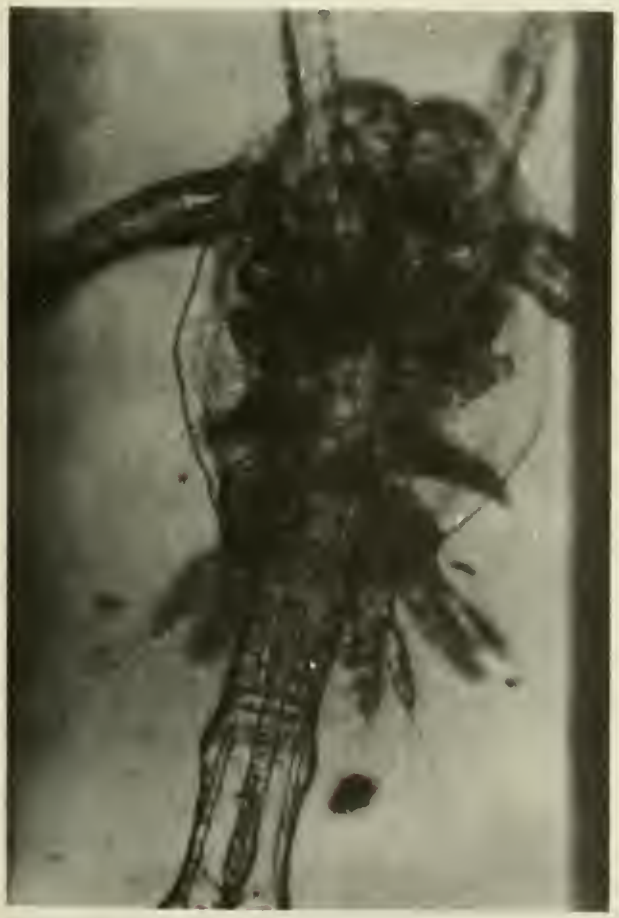

FIGURE 12.—Photomicrograph of first protozoea.

The second maxilla is somewhat larger than the first. It has a protopod of 4 lobed segments. The basal segment bears about 5 setae, and the remaining 3 segments, 2 each. In the protozoeal and mysis stages the setae on the protopod of the maxillae are shorter and stouter than the setae found elsewhere on the body. Each segment of the 5-segmented endopod bears 2 setae except the terminal segment, which has 3. This latter number is constant for the protozoea, but in succeeding stages the scaphognathite increases in size and possesses an increasing number of setae.

The first maxilliped is the largest of the newly functional appendages. It consists of a 2-segmented protopod, a 4-segmented endopod, and an unsegmented exopod. Both of the latter are palplike. The segments of the protopod bear approximately 3 to 4 setae each; those of the endopod have 2 or 3 each except for the terminal segment, which bears 5 setae. The unsegmented exopod bears 7 setae.

The second maxilliped is almost identical to the first, except that it is smaller and bears fewer setae. The protopod has 2 segments and bears approximately 5 to 7 setae. The endopod is 4-segmented; the terminal segment bears 5 setae and the other 3 segments bear 2 setae each. The exopod is unsegmented and bears 6 setae.

The digestive tract runs from the mouth to the posterior end of the body. It is widest at its anterior and posterior portions. A pair of muscle bands is present along the margins of the body in the region of the thorax and abdomen.

SECOND PROTOZOEA

The second protozoeal stage and succeeding larval stages were described from a series of specimens linked with the first protozoea and with each other by their simultaneous occurrence in plankton tows. Individuals of the second protozoeal stage (fig. 13) measured from 1.5 to 1.9 mm. in body length, based on the examination of 15 specimens taken from the plankton.

The main differences between this stage and the preceding one are the acquisition of a rostrum and supraorbital spines, the appearance of stalked compound eyes which are free from the carapace, and the segmentation of the abdomen.

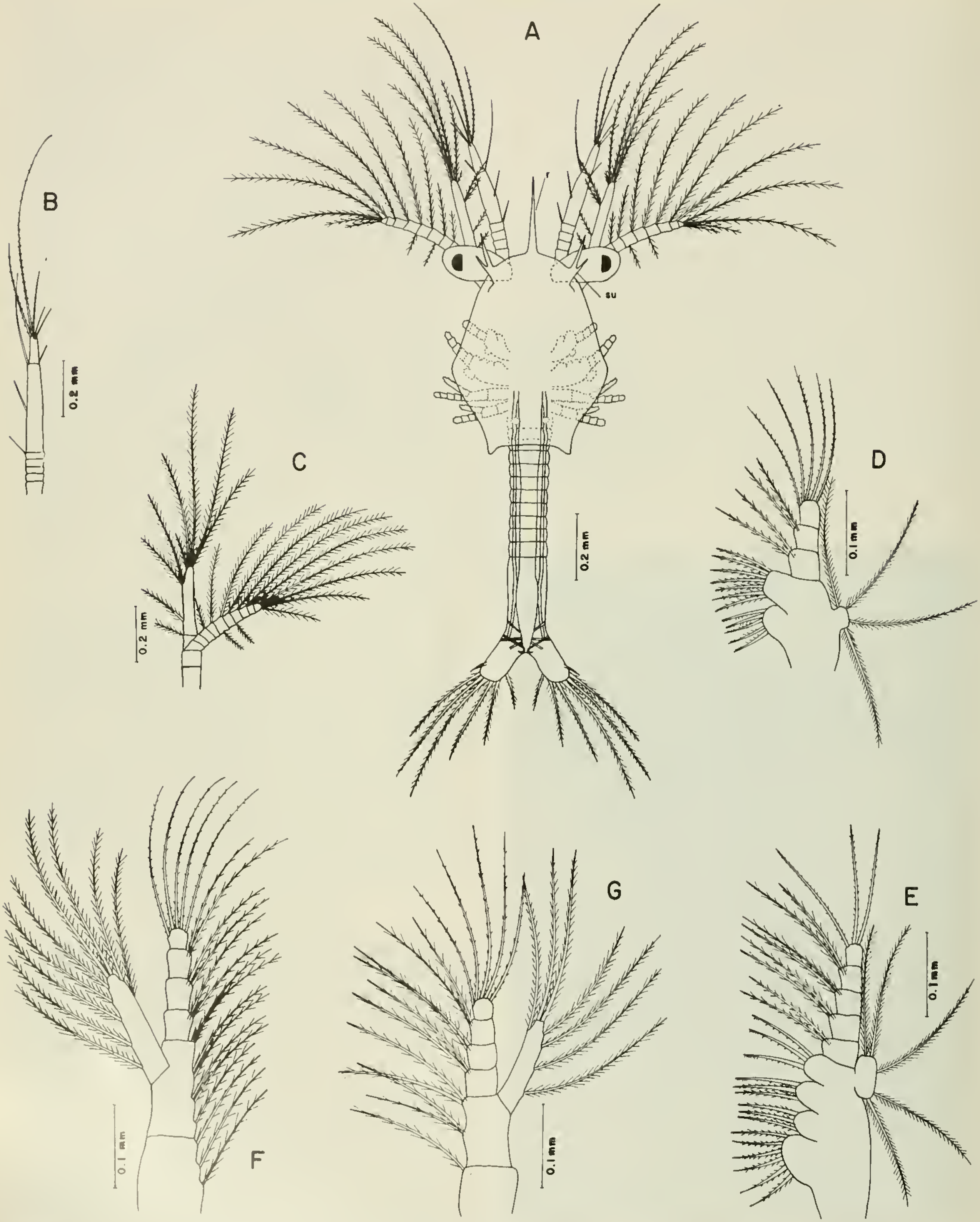

FIGURE 13.—Second protozoea. (A) Dorsal view. (B) First antenna. (C) Second antenna. (D) First maxilla. (E) Second maxilla. (F) First maxilliped. (G) Second maxilliped.

A ventrally curved rostrum is present on the carapace. It measures from one-fourth to one-third the total length of the carapace. The carapace also bears a pair of bifurcated supraorbital spines. It attains its maximum width at about the level of the point of attachment of the second maxillae and then gradually narrows to about half that width. The posterior margin covers the anterior part of the third thoracic somite. The lateral portions of the carapace extend back slightly farther than the dorsal surface.

Gill plates are present for the first time.

There is no great change in the structure of the appendages from those of the first protozoea. A single seta is added to the first antenna. Buds of the thoracic appendages, the third maxillipeds, and the five pairs of pereiopods appear in this stage but are very rudimentary.

The 6 thoracic and 6 abdominal segments are apparent and appear very similar except for the sixth abdominal segment, which is more elongate than the rest. There is no line of demarcation between this segment and the telson.

Each furcal process continues to bear 7 spines.

THIRD PROTOZOEA

Individuals of the third protozoeal stage (fig. 14) measured from 2.2 to 2.7 mm. in body length, based on the examination of 18 specimens taken from the plankton.

The major differences between this and the preceding stage are the appearance of a pair of biramous uropods and of spines on the abdominal somites. All of the somites are fully developed at this stage.

The carapace now covers the first five thoracic somites. The small exterior spines on the supraorbital spines disappear and the latter are thus no longer bifurcated.

The 5 segments of the basal portion of the first antenna are united in this stage. The second antennae, first and second maxillae, and first and second maxillipeds are essentially the same as in the preceding stage. The third maxillipeds and 5 pairs of pereiopods have developed further, but still remain rudimentary and functionless. They all are biramous.

The abdominal somites are now considerably longer than those of the thorax. The sixth abdominal somite is about equal in length to the preceding four combined. The sixth abdominal somite is separated from the telson and differentiation of the body somites is complete. Each of the first 5 abdominal somites bears a dorsomedian spine on its posterior border. In addition, the fifth somite bears a pair of posterolateral spines and the sixth somite bears a pair of posterolateral and a pair of posteroventral spines. All of the spines on the abdominal somites are directed posteriorly.

The biramous uropods are not fully developed. The exopod is somewhat longer than the endopod. The exopod bears 6 short terminal setae and the endopod 2.

There are now 8 spines on each furcal process, with 1 having been added internally to the 7 already existing.

FIRST MYSIS

The second profound metamorphosis occurs at the end of the third protozoeal stage and the larva enters the first mysis stage (fig. 15). Specimens in this stage measured from 2.9 to 3.4 mm., based on the examination of 23 specimens taken from the plankton. The larva now assumes a more familiar shrimplike appearance. The major changes are the development of the thoracic appendages and the nature of the first and second antennae. The carapace, uropods, and telson have also undergone extensive development.

The carapace fits the body more closely than in the protozoeal stages. The smooth rostrum does not curve ventrally in as pronounced a manner as in the preceding stage but projects almost straight forward. There is, however, a good deal of variation in its form. Supraorbital spines are still present, though smaller than in the protozoeal stages. A spine is present at the anteroventral corner of the carapace. A hepatic spine, somewhat removed from the anterior margin of the carapace, is also present. Cephalic and thoracic somites are fused in this stage. The carapace does not quite cover the thorax.

The first and second antennae have changed in form as well as in function: they are no longer natatory, but tactile. The first antenna is divided into 3 segments, the basal segment being equal in length to the other 2 segments. The distal segment bears 2 branches, the external being twice the length of the inner branch. The external branch bears 6 smooth setae and the inner branch 2.

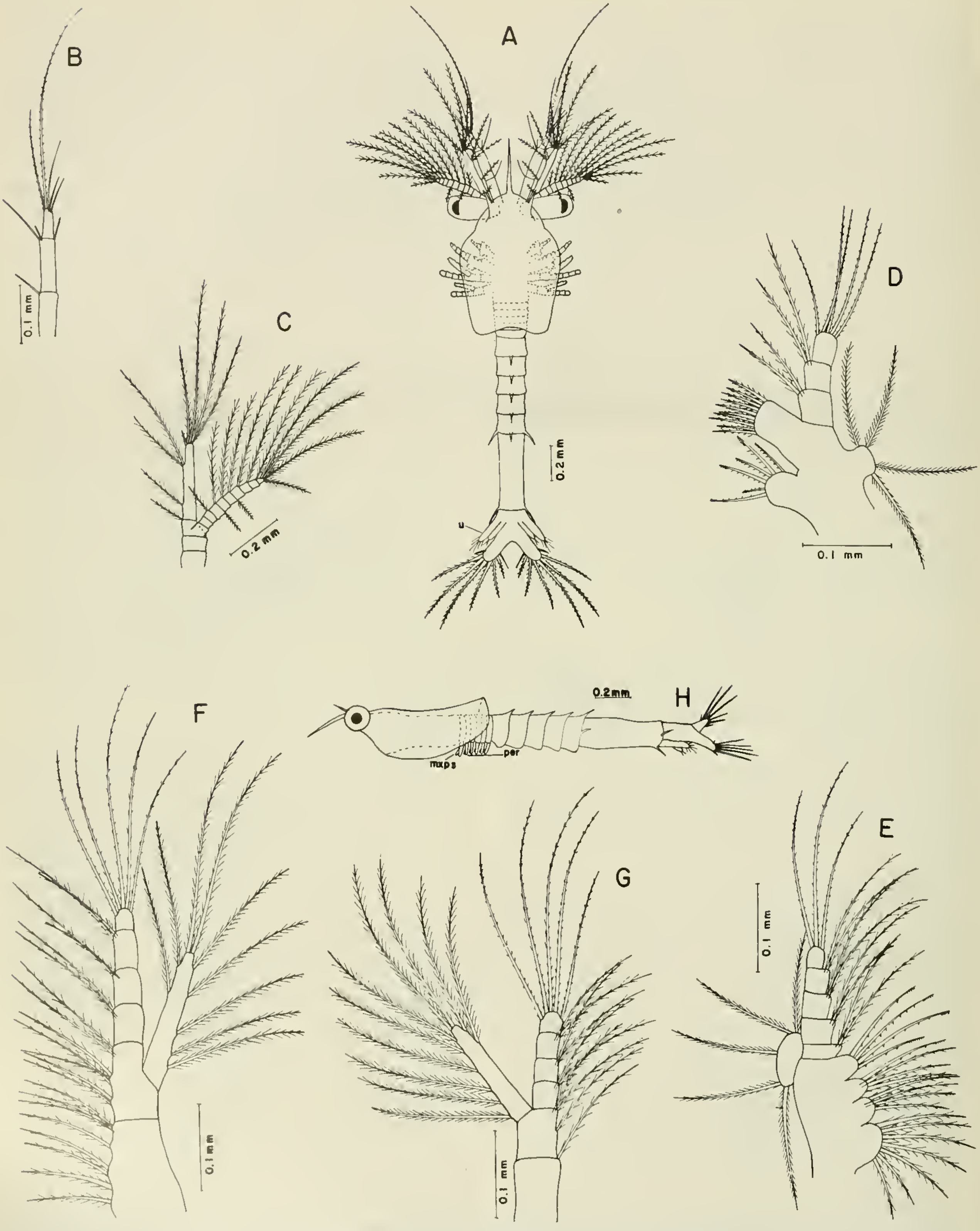

FIGURE 14.—Third protozoea. (A) Dorsal view. (B) First antenna. (C) Second antenna. (D) First maxilla. (E) Second maxilla. (F) First maxilliped. (G) Second maxilliped. (H) Lateral view.

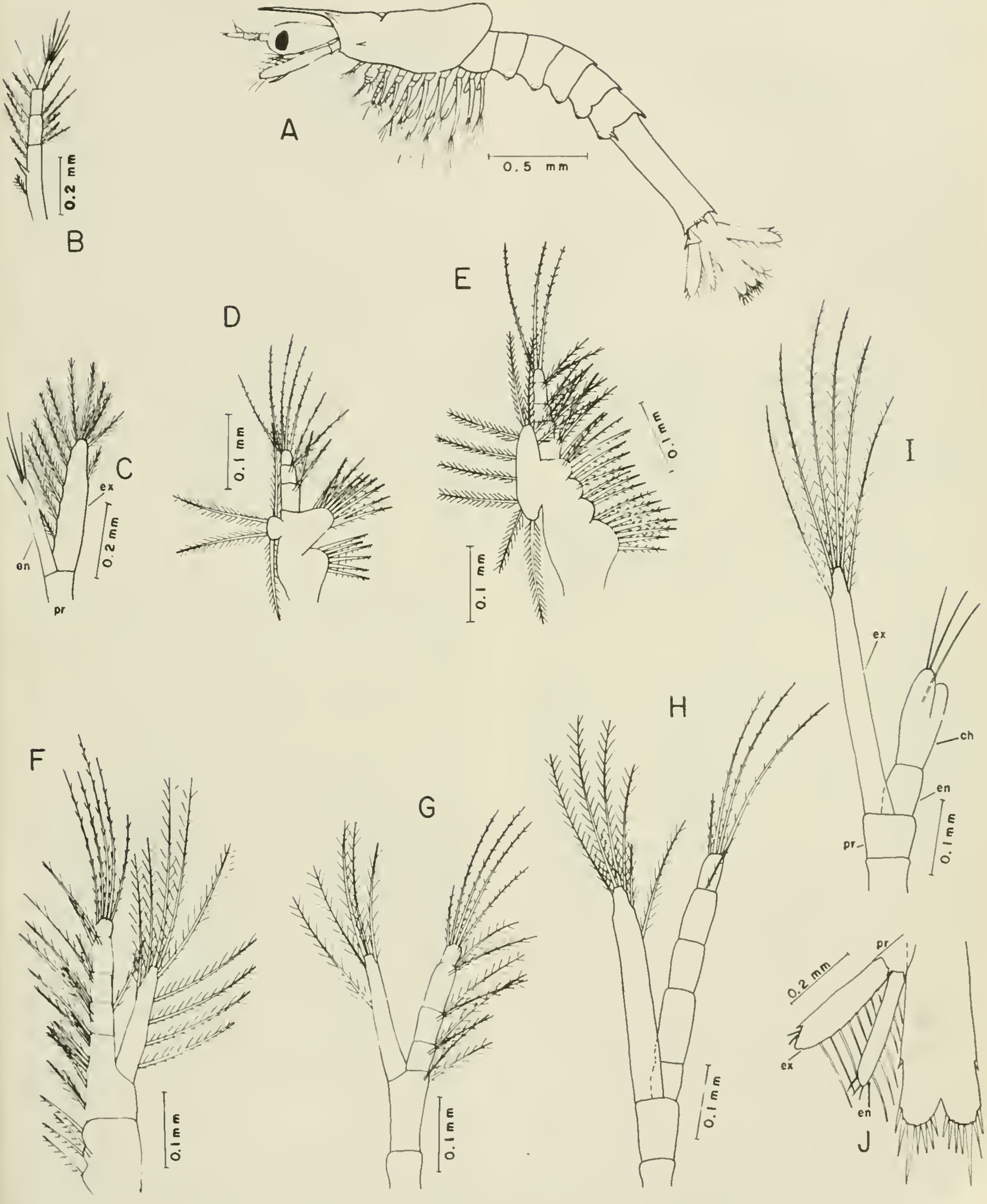

FIGURE 15.—First mysis. (A) Lateral view. (B) First antenna. (C) Second antenna. (D) First maxilla. (E) Second maxilla. (F) First maxilliped. (G) Second maxilliped. (H) Third maxilliped. (I) First pereiopod. (J) Telson and uropod.

There is a series of plumose setae along the margins of the appendage. All of the setae are considerably shorter than in the preceding stage. A large spine is present about midway along the inner margin of the basal segment.

The segments of the exopod of the second antenna have fused to form a flattened scalelike structure. A series of 11 setae is present along the inner and terminal margins, with a twelfth present on the outer margin. The endopod has developed into an unsegmented rodlike structure about two-thirds the length of the exopod. It bears approximately 4 smooth setae, 3 of which are terminal. The protopod consists of 2 segments.

The first and second maxillae are essentially the same as in the preceding stage with the exception that the scaphognathite of the second maxilla has become enlarged and now bears 10 setae. The first and second maxillipeds likewise show no appreciable change.

The third maxilliped is now longer than the first 2. It consists of a 2-segmented protopod, a 5-segmented endopod, and an unsegmented exopod. The endopod bears at least 5 setae, 4 of which are terminal. The exopod bears approximately 6 setae.

The 5 pairs of pereiopods have developed considerably, and are the chief natatory structures of the larva at this stage. In swimming they are assisted by the 3 pairs of maxillipeds. The first 3 pairs of pereiopods are chelate and show a slight increase in size from the anterior to the posterior part of the body. They are composed of a 2-segmented protopod, an endopod of 2 segments (the distal end of the endopod is the rudimentary chela), and an unsegmented exopod. The chela bears 2 or 3 short terminal setae and the endopod 6. The fourth and fifth pereiopods are composed of a 2-segmented protopod, a very short unsegmented endopod, and an unsegmented exopod which is 3 or 4 times the length of the endopod. The endopod bears about 6 terminal setae.

The first and second abdominal segments have lost their dorsal spines, and those of the third and fourth segments are much reduced. The dorsal spines on the fifth and sixth abdominal segments are still fairly prominent. In addition, the fifth segment bears a pair of posterolateral spines, and the sixth segment bears 2 pairs of posterolateral and 1 pair of posteroventral spines and a ventromedian spine on its posterior margin. Buds of the pleopods can be seen on the first 5 abdominal segments.

The uropod now has a protopod which bears 3 spines on its distal border. The exopod and endopod are about equal in length, however, the former is much the wider. The exopod bears about 8 setae on its inner margin, as well as 2 or 3 short setae between the subterminal spine on the outer margin and its distal edge. The endopod bears about 6 lateral and 3 terminal setae.

The telson bears 7 pairs of terminal spines and a pair of small lateral spines. The median notch in the distal margin of the telson is quite well developed, the height of the tip of the notch falling between the lateral and terminal spines. The depth of the notch and the level of its tip in relation to the spines on the telson are important characters in differentiating the three mysis stages.

SECOND MYSIS

Specimens of the second mysis stage (fig. 16) measured from 3.3 to 3.9 mm., based on examination of 8 specimens found in the plankton. The distinguishing characteristic of this stage is the development of rudimentary pleopods.

The carapace now extends back, completely covering the thorax. The appearance of the rostrum and the spination of the carapace are the same as in the preceding stage.

The branches from the distal segment of the first antenna are now almost equal in length. Numerous setae are present at the junction of the segments of the appendage. A bulge, which is the developing statocyst, appears in the basal segment.

A subterminal spine appears on the outer margin of the exopod of the second antenna. The latter bears 8 setae along its inner margin, 4 terminal setae, and 3 setae between the distal tip and the subterminal spine. The endopod remains unsegmented and rodlike, and in this stage is approximately half the length of the exopod. The distal segment of the protopod bears a median spine.

The scaphognathite of the first maxilla has disappeared, while that of the second maxilla has increased in size and now bears 14 setae.

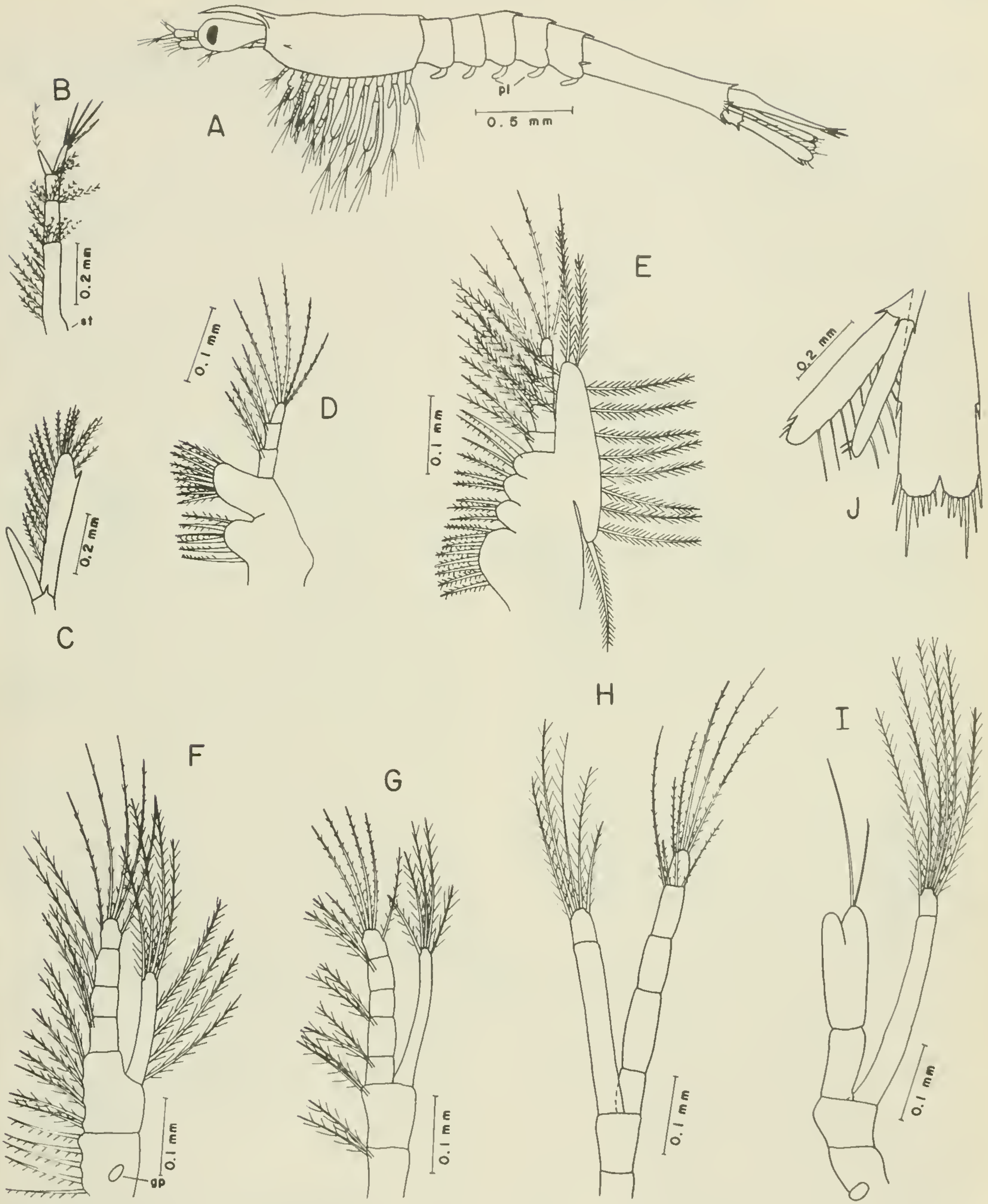

FIGURE 16.—Second mysis. (A) Lateral view. (B) First antenna. (C) Second antenna. (D) First maxilla. (E) Second maxilla. (F) First maxilliped. (G) Second maxilliped. (H) Third maxilliped. (I) First pereiopod. (J) Telson and uropod.

The maxillipeds are much the same as in the preceding stage, except that the exopod of the third maxilliped now has 2 segments.

The pereiopods have grown considerably but their structure remains essentially the same. Of the 3 pairs of chelate pereiopods, the third pair is the longest and the first pair the shortest.

Rudimentary pleopods appear on the abdominal segments in this stage. They are uniramous.

The spination of the abdomen and the appearance of the uropods is the same as in the preceding stage.

The notch at the distal end of the telson is shallower than before. The tip of the notch now reaches only the level of the most external pair of the 7 pairs of terminal spines. The most external 2 pairs of terminal spines are farther apart than in the first mysis.

THIRD MYSIS

Individuals of the third mysis stage (fig. 17) measured from 3.7 to 4.4 mm., based on the examination of 6 specimens taken from the plankton.

The distinguishing characteristics of the third mysis stage are the appearance of a dorsal spine on the rostrum and of well-developed pleopods.

The first and second antennae are much the same as in the second mysis. However, the external branch from the distal segment of the first antenna is now divided into 2 segments. The same is true of the endopod of the second antenna.

The first and second maxillae are essentially the same as in the preceding stage except that the scaphognathite of the latter has continued to increase in size and bears 16 setae.

The endopod of the second maxilliped has 5 segments instead of 4 and the exopod is 3-segmented.

The first 3 pairs of pereiopods are made up of a protopod of 2 segments, an endopod of 4 segments, and an exopod of 2 segments. The endopods of the fourth and fifth pereiopods have 3 or 4 segments, the protopod and exopod 2 each.

The pleopods are well developed although still functionless at this stage. They are divided into 2 segments.

The telson has become somewhat more elongate with the result that the external pair of terminal spines of the second mysis is now in a lateral position. The distal notch has become narrower and shallower, and the height of the tip of the notch is now at the level of the most external of the 6 pairs of terminal spines.

FIRST POSTLARVA

Thirteen specimens of the first postlarval stage measured from 3.8 to 4.8 mm. in body length. All specimens of postlarvae were taken from the plankton.

No great metamorphosis takes place at the molt which gives rise to the first postlarval stage (fig. 18). The pereiopods lose their exopods and the exopods of the maxillipeds are lost or modified. The pleopods take over the swimming function.

The rostrum continues to bear 1 spine near its base and is about equal in length to the eye when the latter is extended forward. The spine at the anteroventral corner of the carapace has disappeared. In most of the specimens examined, the supraorbital spines were absent and a supraorbital crest was developed. In a few cases, however, a small spine remained.

The inner and outer branches from the distal segment of the first antenna now have 2 and 3 segments, respectively. The statocyst at the base of the first antenna is fully developed.

The endopod of the first maxilla is much reduced, unsegmented, and without setae. There is no line of demarcation between it and the peduncle. The same can be said for the endopod of the second maxilla, except that it still has 3 segments. The scaphognathite, which now bears 18 setae, is the dominant structure of the appendage.

Striking changes have taken place in the appearance of the first maxilliped. The endopod is unsegmented, and the exopod has lost its setae. The peduncle has become greatly widened and bears numerous setae along its inner margin.

The second maxilliped has lost its exopod. The endopod consists of 5 segments of which the distal 3 curve inward. The peduncle consists of 2 segments.

The third maxilliped has undergone little change, with the exception of the loss of the exopod. The endopod still has 5 segments and the peduncle 2.

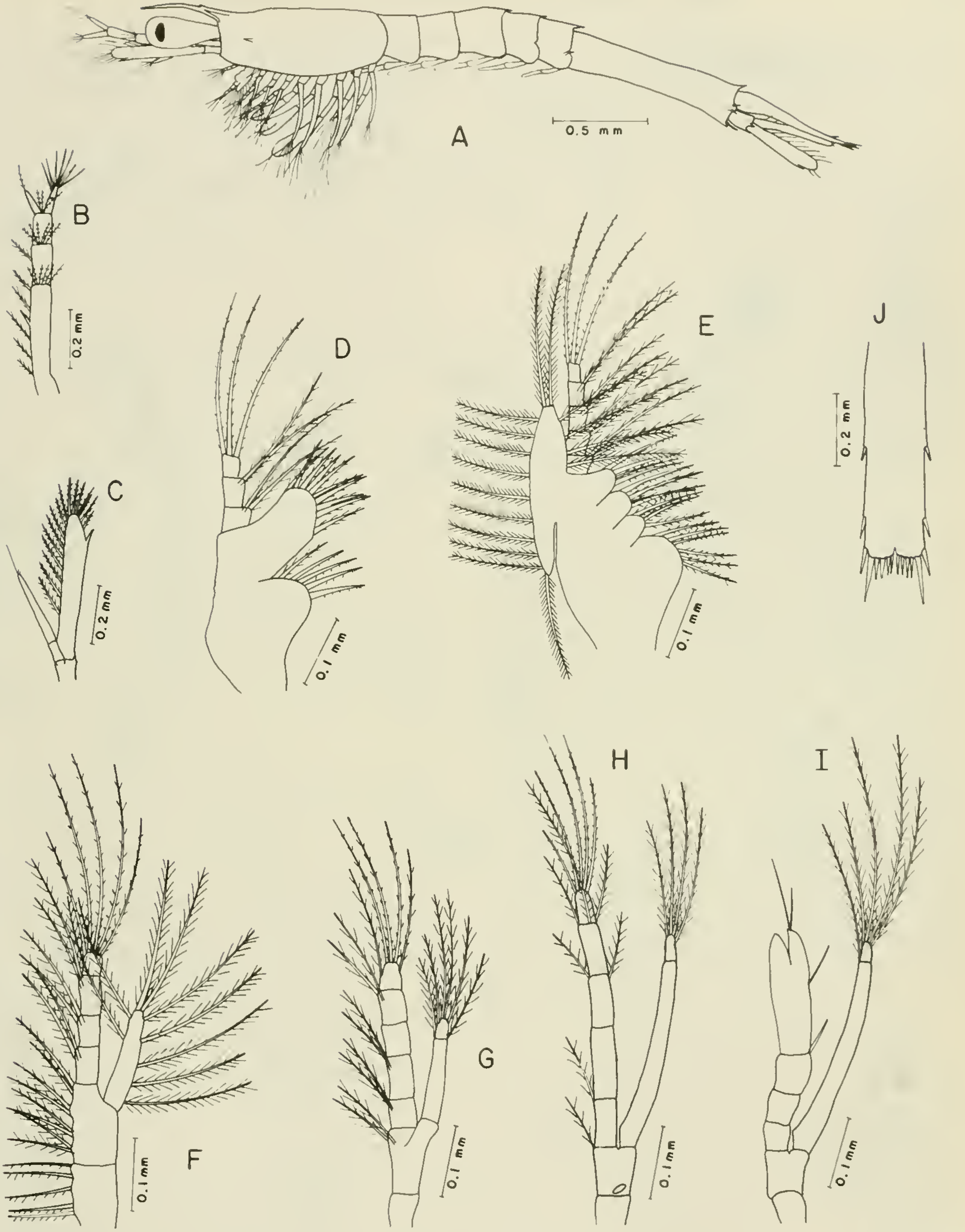

FIGURE 17.—Third mysis. (A) Lateral view. (B) First antenna. (C) Second antenna. (D) First maxilla. (E) Second maxilla. (F) First maxilliped. (G) Second maxilliped. (H) Third maxilliped. (I) First pereiopod. (J) Telson.

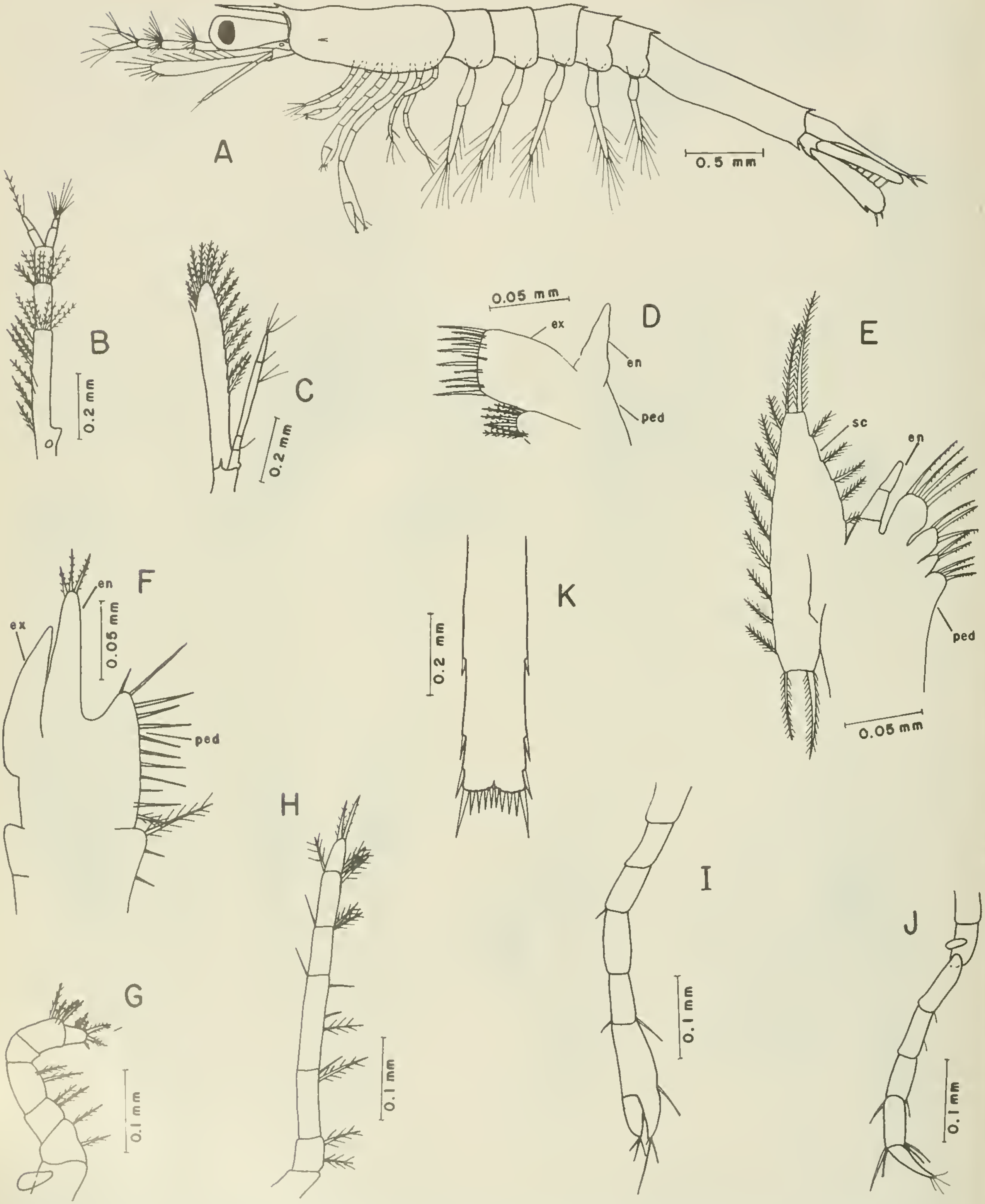

FIGURE 18.—First postlarva. (A) Lateral view. (B) First antenna. (C) Second antenna. (D) First maxilla. (E) Second maxilla. (F) First maxilliped. (G) Second maxilliped. (H) Third maxilliped. (I) First pereiopod. (J) Fourth pereiopod. (K) Telson.

The first 3 pairs of pereiopods consist of a peduncle of 2 segments and an endopod of 5. The chela is formed by the fourth and fifth segments of the endopod. The fourth and fifth pereiopods have the same number of segments as the first three but do not bear chelae. Instead, the fifth segment of the endopod is slightly curved and pointed.

The pleopods have 3 segments, the most distal of which bears about 10 setae. The first three pleopods are better developed than the fourth and fifth.

The dorsal abdominal spines are variable in this stage. Almost all specimens examined had a dorsal spine on the fifth segment. Some had small spines on the third and fourth segments, but others did not. The dorsal spine on the third abdominal segment was the one most often missing. The lateral spines on the fifth abdominal segment were absent on almost all first postlarvae examined, but were present, although reduced, on at least 1 specimen. The 2 pairs of lateral spines on the sixth abdominal segment have disappeared.

The telson is further elongated and now bears 3 pairs of lateral and 5 pairs of terminal spines. The notch is further reduced, its tip falling between the most posterior pair of lateral spines and the terminal spines.

SECOND POSTLARVA

Individuals of the second postlarval stage (fig. 19) measured from 4.7 to 6.6 mm., based on 22 specimens taken from the plankton.

The chief difference between this stage and the first postlarval stage is the presence of a second dorsal spine on the rostrum. In addition, the rostrum is shortened and does not reach the end of the eye when the latter is extended forward.

The inner of the 2 branches from the distal end of the first antenna is now somewhat longer than the external branch and has 3 segments. The flagellum of the second antenna is larger and is composed of 5 segments.

The maxillae are more developed. The scaphognathite of the second maxilla is larger and bears approximately 30 setae.

The endopod of the first maxilliped is much smaller than the exopod, and the mastigobranchial plate has developed greatly. The second maxilliped is curved to a greater degree than in the first postlarva, while the third maxilliped is essentially the same. The same is true of the pereiopods and pleopods.

There are no spines on the third through fifth abdominal segments.

The telson does not differ markedly from the preceding stage. The notch, however, is somewhat less evident.

ADVANCED POSTLARVAE

A series of specimens of postlarvae (fig. 20) from the 3-dorsal rostral-spine stage through the 10-dorsal and 2-ventral rostral-spine stage, measuring from 5.7 to 18.6 mm., was examined (see table 2). From the work of Hudinaga (1942) on *P. japonicus*, it appears probable that several molts occur, with the postlarvae retaining the same number of rostral spines. Hudinaga's observations were made on living material. Although the present study dealt exclusively with preserved material, it was noted that the anteriormost rostral spine of a group of postlarvae having the same number of rostral spines often varied in size. Since this spine is always the one most recently developed, this may be added proof for the supposition that the same number of rostral spines are retained through several molts.

The first ventral spine on the rostrum appears in the stage that has 7 dorsal rostral spines (at approximately 10 to 11 mm.), although the stage or stages preceding it have 7 dorsal and no ventral rostral spines. Likewise, the second ventral spine appears when 8 dorsal spines are present (at approximately 12.5 to 13.5 mm.), although there are specimens with 8+1 rostral spines.

The biramous condition of the pleopods is first clearly evident in the 8+1 stage, but development may have begun in the preceding stage.

TABLE 2.—*Measurements of 48 advanced-stage postlarvae examined*

Number of rostral spines (dorsal+ventral)	Number of specimens examined	Body length, (mm.)
3+0	16	5.7– 7.0
4+0	2	7.2– 7.3
5+0	5	8.1– 9.4
6+0	3	10.2–10.4
7+0	2	9.3– 9.6
7+1	4	10.4–11.3
8+1	4	10.0–11.7
8+2	3	12.5–13.6
9+2	6	[1] 13.7+
10+2	3	[1] 15.5+

[1] Adult *P. duorarum* have 9 or 10 rostral spines.

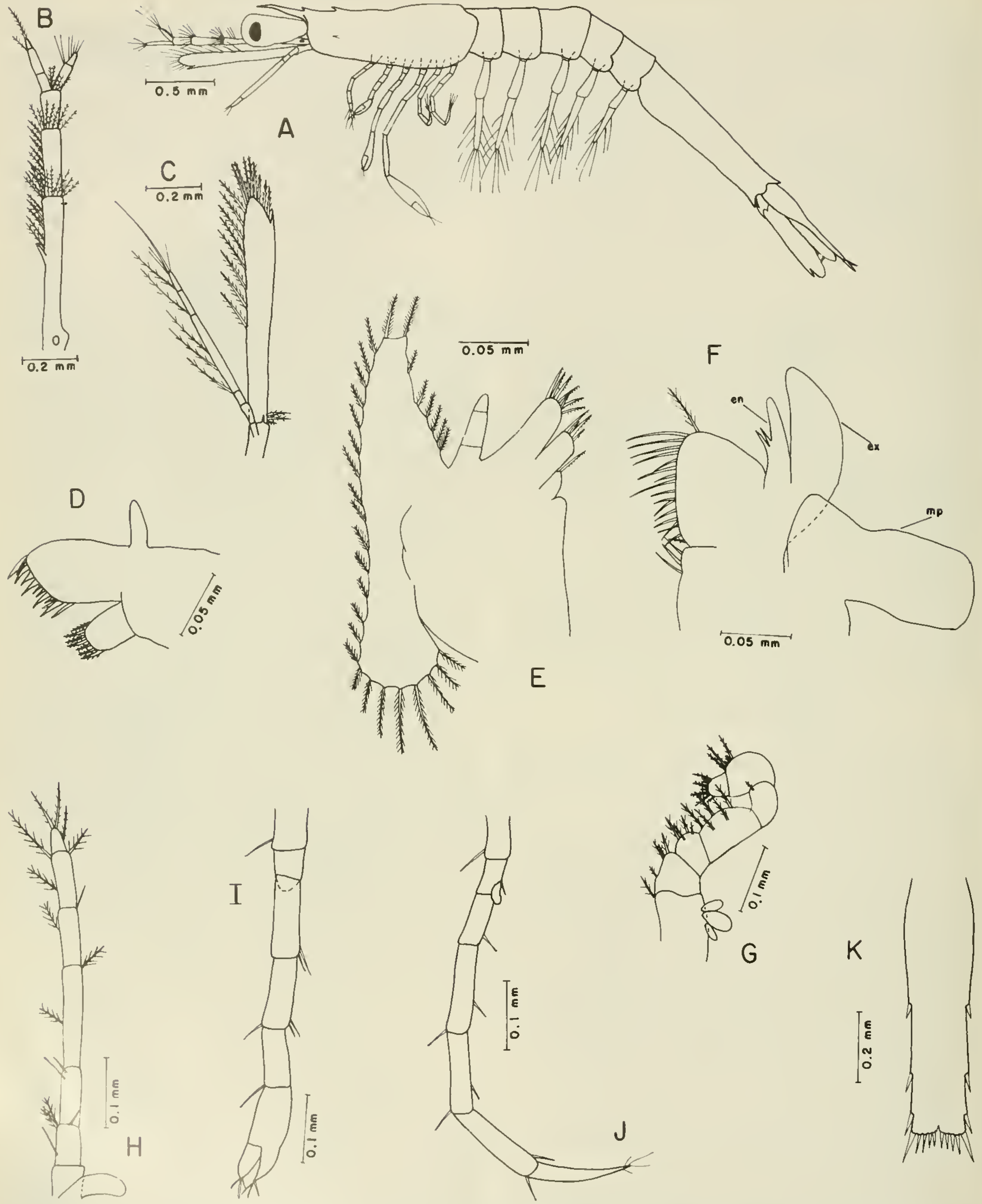

FIGURE 19.—Second postlarva. (A) Lateral view. (B) First antenna. (C) Second antenna. (D) First maxilla. (E) Second maxilla. (F) First maxilliped. (G) Second maxilliped. (H) Third maxilliped. (I) First pereiopod. (J) Fourth pereiopod. (K) Telson.

Development of the carapace is marked by an increase in size of the hepatic spines. An anterolateral spine just ventral to the eye appears in the 7+0-rostral-spine stage and increases in size at each molt thereafter.

The relative lengths of the rostrum and eye differ through the postlarval stages. In the first postlarval stage, the rostrum extends to the edge of the eye or exceeds it in length when the eye is extended forward. The rostrum becomes shortened in the second postlarval stage to about two-thirds the length of the eye, and does not again equal it in length until approximately the 8+2-rostral-spine stage is reached. Thereafter, the rostrum is somewhat longer than the extended eye.

DISCUSSION

The number of stages in each of the phases through which the larvae pass has been found to vary with the species. Hudinaga (1942) reared the larvae of *P. japonicus* through 6 nauplial stages, while Heldt (1938) found 8 in *P. trisulcatus.* Pearson (1939) found 5 nauplial stages in *P. setiferus*, while Heegaard (1953), working only with planktonic material, found 3 stages for the same species. All of these authors found that the species with which they were working passed through 3 protozoeal stages, while 3 mysis stages were observed in *P. japonicus*, 4 in *P. trisulcatus*, and 2 in *P. setiferus*. Broad (1957) noted a variation in the number of larval stages in *Palaemonetes*, depending on the quantity of food available.

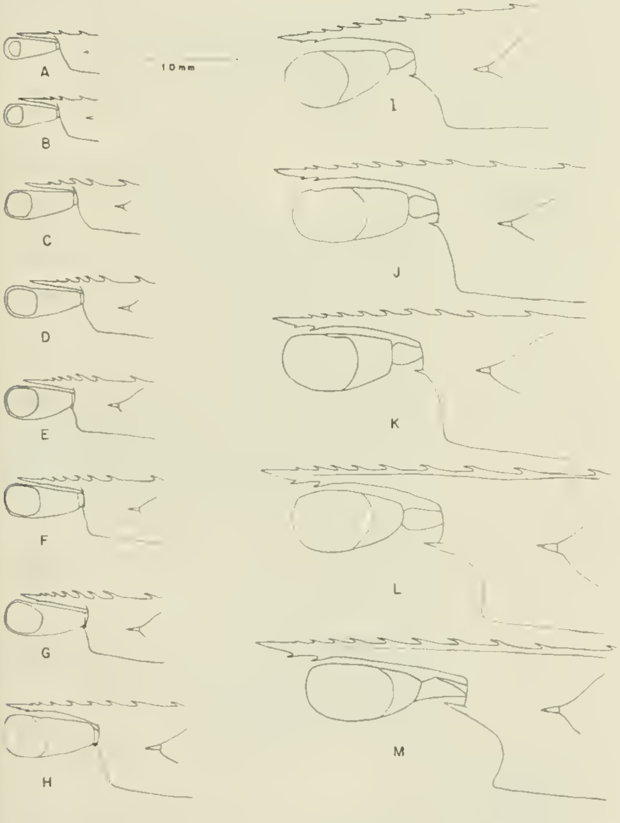

Figure 20.—Carapace and rostrum in advanced postlarvae. (A) 6.9 mm. (B) 7.2 mm. (C) 9.0 mm. (D) 10.2 mm. (E) 9.3 mm. (F) 10.4 mm. (G) 11.1 mm. (H) 12.6 mm. (I) 13.5 mm. (J) 15.5 mm. (K) 15.5 mm. (L) 17.8 mm. (M) 18.6 mm.

COMPARISON WITH *P. SETIFERUS*

The number of nauplial stages found in this study for *P. duorarum* was five, the same as was found by Pearson for *P. setiferus*, but there are slight differences between the corresponding stages of the two species. In the first nauplius, Pearson made no mention of the dorsomedian spine near the posterior end of the body that was noted in *P. duorarum*. Pearson found the second nauplius of *P. setiferus* possessed two pairs of furcal spines. Heegaard described as a first nauplius of the same species a stage which the editors of his paper concluded was a second nauplius because of the appearance of setules on its setae. This stage had a single pair of furcal spines, the condition found in the second nauplius of *P. duorarum.* Pearson found frontal organs on the fourth and fifth nauplial stages, while Heegaard found them on his "last" nauplial stage and first protozoea. Frontal organs were seen only on the fifth nauplius of *P. duorarum;* however, they may also be present on the fourth nauplius.

Of considerable interest is the number of mysis stages. Pearson describes two mysis stages and Heegaard does likewise. An editorial note in Heegaard's paper states, "Heegaard's 'Second Mysis' appears to represent a considerably less advanced stage than Pearson's and it seems probable that there are more than two mysis molts in *P. setiferus* (cf. Heldt, 1938, and Hudinaga, 1942, on other species of *Penaeus*)." This appears true for certain characters, e.g., the absence of a rostral spine, but other structures, such as the telson, appear to be well developed.

Three mysis stages were found in the development of *P. duorarum.* The presence of three stages was based upon the development of the pleopods and the telson as mentioned above. In addition, the third mysis could be distinguished by the presence of a rostral spine.

A comparison of the corresponding stages in the development of *P. setiferus* (based on Pearson's work) and of *P. duorarum* is presented in table 3. The mysis stages were not included since they may not be comparable in the two species.

TABLE 3.—*Corresponding stages in* Penaeus duorarum *and* P. setiferus

[Data on *P. setiferus* from Pearson, 1939]

Stage and structure	*P. duorarum*	*P. setiferus*
Nauplius I:		
Length	0.35–0.40 mm	0.30–0.34 mm.
Width	0.18–0.20 mm	0.16–0.20 mm.
Ocellus	Present	Present.
Labrum	Rounded, ventrally projecting; ends at level of mandible.	Same as in *P. duorarum*.
Antenna I	Uniramous and unsegmented; bears 2 lateral and 3 "terminal" setae (2 terminal and 1 dorsal). Bud of another terminal seta present.	Uniramous and unsegmented; bears 2 lateral and 3 terminal setae.
Antenna II	Biramous and unsegmented. Endopod bears 2 lateral and 2 terminal setae. Bud of another terminal seta present. Exopod bears 3 lateral and 2 terminal setae.	Biramous and unsegmented. Endopod bears 2 lateral and 2 terminal setae. Exopod bears 3 lateral and 2 terminal setae.
Mandible	Biramous and unsegmented. Endopod and exopod bear 3 terminal setae each.[1]	Same as in *P. duorarum*.
Caudal furcae and spines.	Furcae undeveloped. Caudal end bears 1 pair furcal spines. Dorsomedian spine present near posterior end of body.	Furcae and furcal spines the same as in *P. duorarum*. No mention of dorsomedian spine.
Setae	Smooth	Smooth.
Nauplius II:		
Length	0.40–0.45 mm	0.32–0.34 mm.
Width	0.18–0.20 mm	0.16–0.18 mm.
Ocellus	Present	Present.
Labrum	Same as Nauplius I	Same as in Nauplius I.
Antenna I	Unsegmented. Bears 2 setae on anterolateral and 1 on posterolateral surface, and 3 terminal setae.	Same as in *P. duorarum*.
Antenna II	Unsegmented. Endopod bears 2 lateral and 3 terminal setae. Exopod bears 3 lateral and 3 terminal setae.	Same as in *P. duorarum*.
Mandible	Same as Nauplius I	Same as in Nauplius I.
Maxillae and maxillipeds.	Not observed	Faint anlages of first and second maxillipeds appear posterior to mandibles.
Caudal furcae and spines.	Furcal processes undeveloped. Caudal end still bears 1 pair strong furcal spines.	Slight furcal processes, each bears 1 strong and 1 weak furcal spine.
Setae	Longer setae of appendages bear numerous setules.	Same as in *P. duorarum*.
Nauplius III:		
Length	0.45–0.49 mm	0.36–0.40 mm.
Width	0.17–0.20 mm	0.14–0.16 mm.
Ocellus	Present	Present.
Labrum	Same as in preceding stages.	Same as in preceding stages.
Antenna I	Shows signs of segmentation. Bears 2 lateral and 3 terminal setae.	Unsegmented. Setation same as in *P. duorarum*.
Nauplius III—Con.		
Antenna II	Unsegmented. Endopod bears 2 lateral and 3 terminal setae. Exopod bears 3 lateral and 4 terminal setae.	Same as in *P. duorarum*.
Mandible	Same as in preceding stages.	Same as in preceding stages.
Maxillae and maxillipeds.	Not observed	Still under cuticle in midline.
Caudal furcae and spines.	Well-developed. Each furca bears 3 spines.	Same as in *P. duorarum*.
Nauplius IV:		
Length	0.48–0.55 mm	0.38–0.44 mm.
Width	0.18–0.20 mm	0.16–0.18 mm.
Frontal organs	Absent?	Present.
Ocellus	Present	Present.
Labrum	Pointed posteriorly	Same as in *P. duorarum*.
Antenna I	Segmented. Bears 2 lateral and 3 terminal setae.	Same as in *P. duorarum*.
Antenna II	Endopod appears unsegmented and bears 2 lateral and 3 terminal setae. Exopod has about 9 segments and bears 4 lateral and 4 terminal setae.	Endopod may or may not be segmented and bears 2 lateral and 3 terminal setae. Exopod has about 8 segments and bears 4 lateral and 4 terminal setae.
Mandible	Swelling appears in base. Endopod and exopod unsegmented. Setation same as in previous stages.	Same as in *P. duroarum*, except that the endopod appears to be segmented.
Maxillae and maxillipeds.	First and second maxillae and first and second maxillipeds appear externally on ventral surface. Biramous; however, exopods of maxillae knoblike.	First and second maxillae and first and second maxillipeds appear externally on ventral surface. Biramous.
Caudal furcae and spines.	Bear 5 spines each	Same as in *P. duorarum*.
Nauplius V:		
Length	0.53–0.61 mm	0.46–0.56 mm.
Width	0.17–0.20 mm	0.16–0.20 mm.
Frontal organs	Present	Present.
Ocellus	Present	Present.
Labrum	Large and pointed posteriorly.	Same as in *P. duorarum*.
Carapace	Can be seen dorsally under cuticle.	Same as in *P. duorarum*.
Antenna I	Segmented; bears 3 setae on anterolateral and 2 setae on posterolateral surfaces; 3 terminal setae.	Same as in *P. duorarum*.
Antenna II	Endopod bears 3 lateral and 4 terminal setae. Exopod bears 5 lateral and 4 terminal setae.	Endopod bears 2 lateral and 4 terminal setae. Exopod bears 4 lateral and 5 terminal setae.
Mandible	Swelling at base of mandible pronounced; shows spherical masticatory surface. Endopod may or may not be transparent due to lack of musculature.	Swelling at base of mandible pronounced; shows spherical masticatory surface. Endopod transparent due to lack of musculature.
Maxillae	Larger and biramous. Exopods small and knoblike. Endopods bear both terminal and lateral setae. Second maxillae larger than first.	Larger and biramous. Possess short terminal setae. No other description given.
Maxillipeds	Larger and biramous. Exopods typically palplike and bear terminal setae. Endopods bear both terminal and lateral setae.	Larger and biramous. Possess short terminal setae.
Caudal furcae and spines.	Each bears 7 spines. Buds of barbs appear on longer spines.	Each bears 7 spines.
Protozoea I:		
Body length	0.86–1.02 mm. (reared larvae). 0.98–1.14 mm. (from plankton).	0.80–1.14 mm.
Carapace length.	0.40–0.49 mm	0.46 mm. in first protozoea with a body length of 0.86 mm.

See footnote at end of table.

TABLE 3.—*Corresponding stages in* Penaeus duorarum *and* P. setiferus—Continued

TABLE 3.—*Corresponding stages in* Penaeus duorarum *and* P. setiferus—Continued

Stage and structure	*P. duorarum*	*P. setiferus*
Protozoea I—Con.		
Carapace width.	0.35–0.44 mm	0.36 mm. in first protozoea with a body length of 0.86 mm.
Compound eyes.	Developing under carapace.	Same as in *P. duorarum*.
Frontal organs.	Absent	Absent.
Ocellus	Present between developing compound eyes.	Same as in *P. duorarum*.
Labrum	Roughly oval. Anterior edge has large spine; posterior margin slight notch and short bristles.	Anterior edge sharply pointed; posterior edge rounded and covers a section of mandibles.
Labium	2 lobed; extends from under labrum; bristles along median border of lobes.	No description given.
Antenna I	Divided into 3 major segments; with basal segment subdivided into 5 segments. Bears 8 setae.	Same as in *P. duorarum*.
Antenna II	Protopod, 3 segments and without setae. Endopod, 2 segments and 9 setae. Exopod, approximately 10 segments and 13 setae.	Protopod, 2 segments and without setae. Endopod, 2 segments and 8 setae. Exopod, 9 or 10 segments and 12 setae.
Mandible	Has lost endopod and all but trace of exopod. Well-developed masticatory surface.	Mandible modified into flattened plate with serrated edge on inner margin. Both endopod and exopod temporarily lost.
Maxilla I	Protopod has 2 segments; endopod 3. Inner margins of these segments lobed. Exopod (scaphognathite) is budlike. Protopod has about 8 setae, endopod approximately 9, and exopod 4.	Protopod has 2 segments; lobed on inner margins. Each lobe bears about 4 setae. Endopod has 3 segments and bears 8 setae. Several additional outer lateral setae also present on endopod. Exopod (scaphognathite) a small lobe bearing about 2 setae.
Maxilla II	Larger than first maxilla. Protopod has 4 lobed segments and about 10 setae. Endopod has 5 segments with approximately 11 setae. Exopod (scaphognathite) budlike and bears 5 setae.	Larger than first maxilla. Protopod has inner margin divided into 4 small lobes each bearing 2 setae. Endopod has 4 or 5 segments each with pair of setae. Exopod (scaphognathite) knoblike and bears 3 setae.
Maxilliped I	Largest of maxillae and maxillipeds. Protopod has 2 segments (not lobed), each segment bearing 3 to 5 setae. Endopod has 4 segments and about 11 setae. Exopod unsegmented and bears 7 setae. Both endopod and exopod palplike.	Elongate biramous structure. Protopod has 2 segments and 4 setae. Endopod has 9 segments, each segment except distal bearing pair of setae. Distal segment has 4 setae at the tip. Exopod has single segment and bears about 4 lateral and 4 terminal setae.
Maxilliped II	Smaller than first maxilliped. Protopod has 2 segments and about 5 to 7 setae. Endopod has 4 segments and 9 or 10 setae. Exopod unsegmented and bears 6 setae.	Considerably smaller than the first. Protopod has 2 segments and 4 setae. Endopod has 5 segments and 10 setae. Exopod has single segment and bears 7 setae.
Caudal furcae and spines.	Each furca bears 7 spines, the most external of which emanates from dorsal surface. Longer spines bear setules.	Bifurcation of tail stronger than in fifth nauplius. Median notch made by bifurcation is semiovate. 7 spines on each furca.
Digestive tract.	Wider in anterior and posterior portions than between.	Consists of oesophagus, stomach, and intestine and ends in anus which opens somewhat ventrally at the apex of the notch at the posterior end of the body.

The descriptions of the second and third protozoea of *P. setiferus* are not detailed enough to allow a tabular comparison of the two species. The second protozoea measured from 1.5 to 1.9 mm. in *P. duorarum* compared with 1.3 to 1.7 mm. in *P. setiferus*. Measurements of the third protozoea were 2.2 to 2.7 mm. in the pink shrimp and 2.2 to 2.6 mm. in the white shrimp.

From Pearson's drawing (1939: fig. 9, p. 18) it can be seen that the second protozoea of *P. setiferus* lacks a seta at the junction of the distal two segments on the posterolateral margin of the first antenna. The corresponding stage of *P. duorarum* has a short seta at this location. Otherwise, little difference can be noted at this stage between the two species.

The first and second postlarval stages of *P. duorarum* and *P. setiferus* are also very similar on the basis of available descriptions. Pearson reports that the supraorbital spines of the first postlarva are still present, although reduced, while examination of that stage of *P. duorarum* reveals that the spines are almost always missing. Size ranges of these stages are similar.

COMPARISON WITH *P. AZTECUS*

Unfortunately, the larval stages of the brown shrimp, *P. aztecus*, have not been described. Pearson (1939) compared various-sized postlarvae that he originally called *P. braziliensis* (and, in a footnote, tentatively referred them to *P. aztecus*) with similar-sized specimens of *P. setiferus*. He found four principal characters separating the two species in these stages. These characters concern the spination of the rostrum and the relationships of the lengths of the rostrum and the third pereiopod to the length of the eye.

Williams (1959) reviewed the characters described by Pearson and presented a provisional key which could be used to distinguish the postlarvae of *P. setiferus*, *P. aztecus*, and *P. duorarum* under 12 mm. total length. In this key, a difference is noted between the antennal scales of the young postlarvae of the latter two species. In *P. aztecus*, the antennal scale is "nearly uniform in shape with the lateral spine extending beyond the broadly rounded tip," while in *P. duorarum*, "the tip was more or less acutely rounded with the apex near the mesial aspect of the tip. The lateral

---

[1] One of the 3 terminal setae of the exopod actually arises from a constriction in the ramus approximately four-fifths the distance from the body.

spine did not reach the tip." Examination of postlarvae of the two species under 12 mm. total length showed this to be an accurate description.

Williams (1953) compared postlarval and juveniles of *P. setiferus*, *P. aztecus*, and *P. duorarum*. He included drawings of the rostra of 17-, 27-, 37-, and 47-mm. shrimp of the three species; hence the series of rostral drawings of *P. duorarum* were terminated at approximately 18 mm. in this paper.

Lebour (1959) reported larvae of *P. duorarum* in collections made off the coast of tropical West Africa. She figured a 4+0-rostral-spine stage (fig. 1a, p. 141), having well-developed biramous pleopods—a condition not appearing in postlarval *P. duorarum* from Florida waters until the stage in which 8 or 9 dorsal spines are present on the rostrum.

SUMMARY

Four rearing experiments were conducted in which the larvae of *Penaeus duorarum*, the pink shrimp, were raised from eggs obtained from mature females. Young were reared through five nauplial stages and into the first protozoeal stage.

The egg, five nauplial, three protozoeal, three mysis, and two postlarval stages are described and illustrated. In addition, a series of thirteen drawings of the rostra of advanced postlarvae is included. The first six stages were described from specimens raised from eggs, while the remainder of the stages were described from specimens collected from the plankton.

The larval stages of *P. duorarum* are compared with those of *P. setiferus* as described by Pearson (1939). Differences between the postlarvae of *P. duorarum* and *P. aztecus*, as noted by Williams (1959), are discussed.

REFERENCES

Anderson, William W., Joseph E. King, and Milton J. Lindner.

1949. Early stages in the life history of the common shrimp, *Penaeus setiferus* (Linnaeus). Biological Bulletin, vol. 96, no. 2, p. 168–172.

Broad, Alfred Carter.

1957. The relationship between diet and larval development of *Palaemonetes*. Biological Bulletin, vol. 112, no. 2, p. 162–170.

Burkenroad, Martin D.

1939. Further observations on Penaeidae of the Northern Gulf of Mexico. Bulletin Bingham Oceanographic Collection, vol. 6 (art. 6), p. 1–62.

Chin, Edward, and Donald M. Allen.

1959. A list of references on the biology of shrimp (family Penaeidae). U.S. Fish and Wildlife Service, Special Scientific Report—Fisheries No. 276, 143 p.

Costlow, John D., jr., and C. G. Bookhout.

1959. The larval development of *Callinectes sapidus* Rathbun reared in the laboratory. Biological Bulletin, vol. 116, no. 3, p. 373–396.

Dakin, William J.

1938. The habits and life-history of a penaeid prawn (*Penaeus plebejus* Hesse). Zoological Society of London, Proceedings, series A, vol. 108, pt. 2, p. 163–183.

Davis, Harry C., and Robert R. Guillard.

1958. Relative value of ten genera of micro-organisms as foods for oyster and clam larvae. U.S. Fish and Wildlife Service, Fishery Bulletin No. 136, vol. 58, p. 293–304.

Gurney, Robert.

1927. Report on the larvae of the Crustacea Decapoda. Cambridge Expedition to the Suez Canal. Zoological Society of London. Transactions, vol. 22, no. 15, p. 231–286.

1942. Larvae of decapod Crustacea. Ray Society No. 129, 306 p.

1943. The larval development of two penaeid prawns from Bermuda of the genera *Sicyonia* and *Penaeopsis*. Zoological Society of London, Proceedings, series B, vol. 113, p. 1–16.

Heegaard, Poul E.

1953. Observations on spawning and larval history of the shrimp, *Penaeus setiferus* (L.). University of Texas, Publications of the Institute of Marine Science, vol. 3, no. 1, p. 73–105.

Heldt, Jeanne H.

1938. La reproduction chez les Crustacés Décapodes de la famille des Pénéides. Annales de l'Institute Oceanographique de Monaco, vol. 18 (fasc. 2), p. 31–206.

Hudinaga, Motosaku.

1942. Reproduction, development and rearing of *Penaeus japonicus* Bate. Japanese Journal of Zoology, vol. 10, no. 2, p. 305–393.

Johnson, Malcolm C., and J. R. Fielding.

1956. Propagation of the white shrimp, *Penaeus setiferus* (Linn.), in captivity. Tulane Studies in Zoology, vol. 4, no. 6, p. 173–190.

Lebour, Marie V.

1959. The larval decapod Crustacea of tropical West Africa. "Atlantide" Report No. 5, p. 119–143, fig. 1a.

MENON, M. KRISHNA.

1952. The life history and bionomics of an Indian penaeid prawn *Metapenaeus dobsoni* Miers. Indo-Pacific Fisheries Council, Proceedings, Third Meeting, Section 2, p. 80–93.

MORRIS, MURIEL C., and ISOBEL BENNETT.

1952. The life history of a penaeid prawn (*Metapenaeus*) breeding in a coastal lake (Tuggerah, New South Wales). Proceedings, Linnaean Society of New South Wales, vol. 76, nos. 5–6, p. 164–182.

PEARSON, JOHN C.

1939. The early life histories of some American Penaeidae, chiefly the commercial shrimp, *Penaeus setiferus* (Linn.). U.S. Bureau of Fisheries, Bulletin 30, vol. 49, p. 1–73, figs. 2–18, 21–30.

WEYMOUTH, FRANK W., MILTON J. LINDNER, and WILLIAM W. ANDERSON.

1933. Preliminary report on the life history of the common shrimp, *Penaeus setiferus* (Linn.). U.S Bureau of Fisheries, Bulletin 14, vol. 48, p. 1–26.

WILLIAM, AUSTIN B.

1953. Identification of juvenile shrimp (Penaeidae) in North Carolina. Elisha Mitchell Scientific Society, Journal, vol. 69, no. 2, p. 156–160, figs. 1 and 2.

1955. A contribution to the life histories of commercial shrimps (Penaeidae) in North Carolina. Bulletin of Marine Science of the Gulf and Caribbean, vol. 5, no. 2, p. 116–146.

1959. Spotted and brown shrimp postlarvae (*Penaeus*) in North Carolina. Bulletin of Marine Science of the Gulf and Caribbean, vol. 9, no. 3, p. 281–290, figs. 1–3.

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SEROLOGICAL STUDIES OF ATLANTIC REDFISH

BY CARL J. SINDERMANN

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ABSTRACT

Individual variations in erythrocyte antigens have been found in redfish, *Sebastes marinus*, from the western North Atlantic. Two closely related antigens, tentatively labeled A_1 and A_2, were demonstrated with specific reagents created by absorptions of rabbit antisera. Each reagent would agglutinate cells of only one antigenic type, so it was possible to identify fish as possessing A_1 or A_2 antigen. Individuals with the erythrocyte antigen A_1 make up more than 75 percent of the Eastport (Maine) redfish population. Since antigen frequencies may vary from one population to another, quantitative studies of each major fishing area should provide further information about discreteness of groups and the extent of their movements.

SEROLOGICAL STUDIES OF ATLANTIC REDFISH

By Carl J. Sindermann, *Fishery Research Biologist*

Bureau of Commercial Fisheries

Knowledge of the population structure of commercial marine fish species is important as a basis for management. Traditionally, information about intraspecies groups has been derived from morphometric and meristic studies, tagging, or age and growth studies. Valuable data have been obtained through the use of such methods, and it seems reasonable that the greater the number of criteria used, the more accurate will be the conclusions. For this reason, and because of the ultimate need for genetic information about intraspecies groups, attention has been directed recently toward serological methods of population analysis, and particularly toward blood-group research. Serological studies of marine fishes (Cushing, 1952, 1956; Ridgway, 1957; Ridgway, Cushing, and Durall, 1958; Suzuki, Shimizu, and Morio, 1958; Sindermann and Mairs, 1959; Ridgway and Klontz, 1960) have demonstrated individual differences in red-blood-cell antigens, and, in some studies quantitative differences in the frequency of occurence of antigens in different populations. Knowledge of such differences should prove as useful in fishery investigations concerned with population or racial problems as that of the racial distribution of human blood groups has to anthropological studies.

Before quantitative studies are possible, however, the often slow but always essential development of blood-group systems and standardization of reagents for their demonstration must be carried out. This paper is concerned with the recognition and description of blood-group antigens in redfish, *Sebastes marinus* (L.), which in recent years has become a commercially valuable species in the western North Atlantic. Attention has been directed to this fish because of confusion about certain morphologically recognizable groups which are possibly of subspecies stature, and because of a lack of knowledge concerning the population structure within these groups. Such problems should be amenable to serological investigation: the blood group antigens described here represent a first, tentative, but necessary step in this process.

METHODS

Samples of redfish blood were obtained from Eastport, Maine, and Georges Bank in the southern Gulf of Maine. Blood was taken directly from the heart; cells for testing were washed from clots with a 1.4 percent saline solution and were used in approximately 4 percent suspensions. Antisera were prepared in rabbits and chickens by injections of individual and pooled samples of washed redfish blood cells diluted 1:1 with saline. Usually, a single, short injection series was used to develop as specific antisera as possible. Six injections of 1 milliliter each were given on alternate days. Rabbits were trial bled 10 days after the last injection, and, if the antiserum titer proved satisfactory, food was withheld and the animals were bled terminally on the following day. Rabbit antisera were also prepared by injecting red cells of cod, herring, alewife, lamprey, and sheep.

Cell agglutination tests were made at room temperature within 72 hours from the time the fish blood was taken, although reactions of refrigerated cells did not change noticeably up to 7 days. Tube agglutination tests used 0.2 ml. antiserum dilution and 0.05 ml. cell suspension. Readings were taken after 15 minutes incubation at room

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temperature and 30 seconds centrifugation. In the preparation of specific agglutinating reagents, antisera were absorbed by incubating one part redfish cells and four parts diluted antiserum for 10 minutes at room temperature. One absorption was usually sufficient to remove all antibodies reactive with the absorbing cells. Reagents and antisera were frozen in 3-ml. aliquots which were thawed and heat-inactivated just before use to destroy complement.

RESULTS

Rabbit antisera prepared by injecting pooled and individual samples of redfish cells provided the first indication of individual differences in redfish erythrocytes. At appropriate dilutions of these antisera, cells of certain fish reacted weakly, while cells of other fish were strongly positive. As an example, a rabbit antiserum (labeled GBR17R), prepared by injecting pooled cells of 14 Georges Bank redfish, agglutinated cells of certain redfish from a small sample taken at Eastport, Maine, to a titer of 1:128, while cells from other fish in the same sample were not agglutinated beyond the 1:32 dilution (table 1). The degree of agglutination was recorded conventionally in descending order from (++++), representing complete agglutination, to (−), indicating no agglutination.

Table 1.—*Reactions of rabbit anti-redfish serum (GBR17R) with erythrocytes of six individual Eastport redfish*

Antiserum GBR17R dilutions	Degree of agglutination of erythrocytes from individual redfish					
	No. 1	No. 2	No. 3	No. 4	No. 5	No. 6
1:8	++	++++	++++	++	++++	++++
1:16	++	+++	+++	++	++++	+++
1:32	+	++	++	+	+++	++
1:64	−	+	+	−	++	+
1:128	−	+	−	−	+	+

Cells from fish Nos. 1 and 4 reacted weakly with the antiserum, while cells of other fish reacted more strongly. This suggestion of individual differences in redfish erythrocyte antigens was supported by absorptions of the antiserum. Results of absorbing with cells from each of the fish mentioned above are presented in table 2.

Table 2.—*Results of absorbing*[1] *rabbit anti-redfish serum (GBR17R) with erythrocytes of six individual Eastport redfish*

Antiserum (GBR17R) diluted 1:4 and absorbed with erythrocytes of individual redfish	Degree of agglutination of erythrocytes from individual redfish					
	No. 1	No. 2	No. 3	No. 4	No. 5	No. 6
No. 1	−	+	++	−	+	+
No. 2	−	−	−	−	−	−
No. 3	−	−	−	−	−	−
No. 4	−	+	+	−	+	+
No. 5	−	−	−	−	−	−
No. 6	−	−	−	−	−	−
Unabsorbed	++	++++	++++	++	++++	++++

Absorption of the antiserum with cells of fish Nos. 2, 3, 5, and 6 removed antibodies for absorbing cells and for all others, while absorption with cells of fish Nos. 1 and 4, which reacted weakly with unabsorbed antiserum, removed antibodies for each other, but left antibodies which agglutinated cells of fish Nos. 2, 3, 5, and 6. Comparison of cell agglutinations with absorbed and unabsorbed antiserum indicated that absorptions drastically reduced the antibody content. The tests demonstrated antigenic dissimilarity in redfish erythrocytes, but suggested that the antigens were closely related. As a descriptive measure, fish whose cells reacted strongly with unabsorbed antiserum, and also removed antibodies for all other cells in absorptions, were considered as possessing an antigen A_1, while those fish whose cells reacted weakly with the unabsorbed antiserum, and did not remove antibodies for A_1 cells in absorptions, were considered as possessing an antigen A_2.

Referring again to table 2, weakly reacting cells of fish Nos. 1 and 4 would thus be A_2, while strongly reacting cells of fish Nos. 2, 3, 5, and 6 would be A_1. Using a reagent prepared by absorbing the GBR17R antiserum with cells of A_2 fish, it was possible to recognize fish of each antigenic type, since only cells of fish with A_1 antigen were agglutinated.

Confirmation of this system was possible with a rabbit antiserum (labeled MIC8R) which had been prepared for another study by injecting pooled cod cells. Individual differences were slight with the unabsorbed antiserum, but absorption with cells of the six fish used previously produced results shown in table 3.

Absorption with cells of fish Nos. 1 and 4 removed antibodies for absorbing cells and for all

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[1] Absorptions of specific antibodies were made by incubating one part redfish cells and 4 parts diluted (1:4) antiserum for 10 minutes at room temperature. After this period, the absorbing cells were centrifuged and the supernatant fluid tested against an aliquot of the cells used for absorption. One absorption was usually sufficient to remove all antibodies reactive with antigens of the absorbing cells.

TABLE 3.—*Results of absorbing rabbit anti-cod serum (MICSR) with erythrocytes of six individual Eastport redfish*

Antiserum MICSR diluted 1:4 and absorbed with erythrocytes of individual redfish	Degree of agglutination of erythrocytes from individual redfish					
	1 (A_2)	2 (A_1)	3 (A_1)	4 (A_2)	5 (A_1)	6 (A_1)
No. 1	–	–	–	–	–	–
No. 2	+	–	–	+	–	–
No. 3	+	–	–	+	–	–
No. 4	–	–	–	–	–	–
No. 5	+	–	–	+	–	–
No. 6	+	–	–	+	–	–
Uuabsorbed	++	+++	+++	++	++++	+++

others, while absorption with cells of fish Nos. 2, 3, 5, and 6 removed antibodies for each other but left antibodies which agglutinated cells of fish Nos. 1 and 4. These reactions were reciprocals of those obtained by absorbing the anti-redfish (GBR17R) serum. They immediately suggested that the anti-cod (MICSR) was principally an anti-A_2 serum, while the anti-redfish (GBR17R) was principally an anti-A_1 serum. Therefore, by absorbing the MIC8R antiserum with A_1 cells (No. 2, 3, 5, and 6, and others with similar reaction), a reagent was obtained which reacted only with A_2 cells. This provided two reagents, one (prepared previously by absorbing GBR17R antiserum with A_2 cells) which agglutinated only cells with A_1 antigen; the other (prepared by absorbing MIC8R antiserum with A_1 cells) which agglutinated only cells with A_2 antigen. It was then possible to definitely identify fish as possessing either antigen A_1 or A_2.

Since the original stock of MIC8R antiserum was small, other specific anti-redfish sera were prepared. Rabbits were immunized with cells of individual redfish previously tested for A antigens. Two antisera (GBR31R and GBR32R) were especially useful in preparation of specific A_1 reagents. Results of absorptions of GBR31R antiserum are illustrated in table 4. More than 75 percent of redfish sampled thus far from the Eastport (Maine) population possessed antigen A_1. Future work logically involves testing large numbers of individuals from each major fishing area to determine whether variations in antigen frequencies exist. If such variations occur, the maximum amount of intermixing could be determined.

DISCUSSION

Blood-group antigens of the kind considered in this paper have been most thoroughly studied in mammals and birds. Blood-group systems have been proposed for humans, cattle, whales, chickens, and certain other animals. Wherever studied, the erythrocyte antigens composing these systems have been found to be genetically determined, with relatively simple inheritance usually involving a single locus. Comparable studies of fishes are still in their infancy, but should be as useful to studies of fish populations and migrations as human blood groups are to anthropological studies, or as blood groups of cattle are to herd-lineage problems. Information derived is genetic, and may provide a more adequate picture of the population structure of a species than is possible with morphological criteria, many of which are subject to modification by environmental factors.

From research in this laboratory (Sindermann and Mairs, 1959) and that reported from elsewhere (Cushing, 1956; Ridgway, Cushing, and Durall, 1958; Suzuki, Shimizu, and Morio, 1958; and others), it is already apparent that individual variations in erythrocyte antigens characterize

TABLE 4.—*Results of absorbing rabbit anti-redfish (anti A_1) serum (GBR31R) with cells of 12 Eastport (Maine) redfish*

Antiserum GBR31R absorbed with cells of redfish	Degree of agglutination of erythrocytes from individual redfish											
	61(A_1)	62(A_2)	63(A_1)	64(A_1)	65(A_1)	66(A_1)	67(A_2)	68(A_1)	69(A_2)	70(A_1)	71(A_1)	72(A
No. 61	–	–	–	–	–	–	–	–	–	–	–	–
No. 62	+++	–	++++	++	+++	+++	–	+++	–	+++	++	+++
No. 63	–	–	–	–	–	–	–	–	–	–	–	–
No. 64	–	–	–	–	–	–	–	–	–	–	–	–
No. 65	–	–	–	–	–	–	–	–	–	–	–	–
No. 66	–	–	–	–	–	–	–	–	–	–	–	–
No. 67	+	–	++	+	+	+	–	++	–	+	+	+++
No. 68	–	–	–	–	–	–	–	–	–	–	–	–
No. 69	+	–	++	+	+	+	–	++	–	+	+	++
No. 70	–	–	–	–	–	–	–	–	–	–	–	–
No. 71	–	–	–	–	–	–	–	–	–	–	–	–
No. 72	–	–	–	–	–	–	–	–	–	–	–	–
Unabsorbed	++++	++	++++	++++	++++	++++	++	++++	++	++++	+++	++++

teleosts as well as other vertebrate groups. Recent findings of Suzuki, Shimizu, and Morio (1958), Sindermann and Mairs (1959), and Ridgway and Klontz (1960) suggest that geographic variation in antigen frequencies can also be expected. If this is generally true, such variations may prove important to population or racial studies of marine fishes.

The A blood-group antigens of redfish described in this paper represent a first phase in serological characterization of this important marine fish species. Future work should include quantitative studies of the distribution of A-group antigens in redfish from widely separated areas, to see whether there is variability in their frequencies. Furthermore, search should be continued for other blood-group antigens in the species, since adequate serological characterization may depend on several such criteria. Just as in humans it is possible to make major racial separations based on the ABO blood-group system alone, so an initial redfish population analysis may be based only on the A antigens. However, more precise population subdivisions and indications of past migrations of humans have emerged from studies of several blood-group systems, and more complete understanding of redfish populations could depend on identification, description, and use of more than one system. The initial serological step has been taken, with encouraging results, but more information on a much broader scale is necessary.

Use of the varied approaches available to serology, including study of serum and egg proteins as well as erythrocyte antigens comparable to those described here, should provide further data for fish systematic studies, both above and below the species level. It should be emphasized however that no single approach to problems of subspecies, races, or subpopulations can be a panacea. Serology may constitute one of several criteria in such analyses, along with traditional morphometric and meristic studies, but a final synthesis should include data from diverse methods of investigation. It does seem, though, that once techniques have been sufficiently standardized, serology will provide a powerful tool for biological studies of such commercially valuable species as the redfish.

CONCLUSIONS AND SUMMARY

Individual differences in erythrocyte antigens have been found to exist in redfish. Detection of such differences was possible with absorbed rabbit anti-redfish and anti-cod serum.

Based on results of antiserum absorptions, two closely related antigens, A_1 and A_2 have been identified. Reagents were prepared which specifically agglutinated cells possessing each antigen.

Using the reagents prepared by absorptions of antisera, it has been found in limited sampling that redfish possessing the erythrocyte antigen A_1 make up more than 75 percent of the Eastport (Maine) population.

Quantitative studies of antigen frequencies in samples from each major fishing area should provide information about the intraspecies structure of redfish.

LITERATURE CITED

Cushing, John E.

1952. Serological differentiation of fish bloods. Science, vol. 115, No. 2989, p. 404–405.

1956. Observations on the serology of tuna. U.S. Fish and Wildlife Service, Special Scientific Report—Fisheries No. 183, 14 p.

Ridgway George J.

1957. The use of immunological techniques in racial studies. U.S. Fish and Wildlife Service, Special Scientific Report—Fisheries No. 208, p. 39–43.

Ridgway, George J., J. E. Cushing, and G. L. Durall.

1958. The serological differentiation of populations of sockeye salmon (*Oncorhynchus nerka* Walbaum). U.S. Fish and Wildlife Service, Special Scientific Report—Fisheries No. 257, 9 p.

Ridgway, George J., and George W. Klontz.

1960. Blood types in Pacific salmon. U.S. Fish and Wildlife Service, Special Scientific Report—Fisheries No. 324, 9 p.

Sindermann, Carl J., and Donald F. Mairs.

1959. A major blood group system in Atlantic sea herring. Copeia, 1959, No. 3, p. 228–232.

Suzuki, Akimi, Yasuyuki Shimizu, and Tado Morio.

1958. Serological studies of the races of tuna. I. The fundamental investigations and the blood groups of albacore. Nankai Regional Fisheries Research Laboratory (Japan), Report No. 8, p. 104–116.

UNITED STATES DEPARTMENT OF THE INTERIOR, Stewart L. Udall, *Secretary*
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ESTIMATING RED SALMON ESCAPEMENTS BY SAMPLE COUNTS FROM OBSERVATION TOWERS

BY CLARENCE DALE BECKER

March 3, 1849

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ABSTRACT

The method of estimating red-salmon escapements used from 1955 to 1959 on the Kvichak River (Alaska) involved taking visually systematic sample counts as the fish passed observation towers beside the paths of migration. The counts followed a sampling design which fluctuated in extent of coverage with the intensity of the run. This report describes in detail the method of sampling and calculating the escapement estimates, summarizes the counts for each year, and discusses the accuracy of the estimates.

ESTIMATING RED SALMON ESCAPEMENTS BY SAMPLE COUNTS FROM OBSERVATION TOWERS

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The Kvichak River system of western Alaska is the foremost producer of red or sockeye salmon, *Oncorhynchus nerka* (Walbaum), for the Bristol Bay commercial fishery. Since 1955, a series of biological investigations on the red salmon of this system has been conducted by the Fisheries Research Institute of the University of Washington. A major aspect of the investigation has been to estimate the numbers of adult red salmon which compose the annual spawning escapement.

The method of estimation developed by the Institute involves systematic visual sample counts of the transient bands of migrants, taken in the main river after the fish have passed through the fishery and before they have dispersed throughout the spawning grounds. When the numbers of fish in the commercial catch are added, the total return can be determined. In addition, when the data are coupled with age analysis of scale samples from both the catch and the escapement, accurate estimates can be made of the number of adults in each age group returning from a given year of spawning and from a given year of seaward migration.

It is the purpose of this report to: (1) describe in detail the counting method, (2) summarize the counts from the years 1955 to 1959, and (3) discuss the factors influencing the estimation. The techniques discussed are the results of 5 years of research on the Kvichak.

This method of estimating a salmon escapement from tower counts made from observation towers in Bristol Bay, Alaska, was proposed by W. F. Thompson in the spring of 1953, and he organized the initial experiment on the Wood River in that same summer (Fisheries Research Institute, 1955; Thompson and Clancy, 1959). The success of this method prompted repetition the following year, with expansion to the Kvichak River system in 1955. In 1956 and 1957, the Bureau of Commercial Fisheries, U.S. Fish and Wildlife Service, compared estimates from tower counts with those from the weirs on the Egegik River and found insignificant differences in total numbers of fish (Bureau of Commercial Fisheries, 1956 and 1957). In 1957, for the first time the escapements to all major red salmon streams in Bristol Bay were assessed from intermittent visual counts made from towers along the river banks.

The Kvichak River is about 57 miles long, draining from Iliamna Lake and following a twisting course through flat tundra country before flowing into Kvichak Bay (fig. 1). Its lower 43 miles is influenced by tides and the river has a mean depth of about 10 feet. From the head of tidewater, a broad area of numerous shallow channels called the Kaskanak Flats extends upriver 8 miles. From the flats to the outlet of Iliamna Lake, a distance of 4 miles, the river is restricted to a deeper channel that contains a few islands and gravel bars.

The system drains a watershed of 7,700 square miles, which includes a profusion of lakes and connecting or tributary streams. Iliamna Lake alone is 77 miles long and from 8 to 20 miles wide. Clark Lake, connected to Iliamna Lake by the Newhalen River, is 52 miles long and from 1 to 4 miles wide (U.S. Army Corps of Engineers, 1957). Extensive red salmon spawning grounds are distributed in streams, in spring ponds, and on beaches throughout the area.

As the Kvichak River empties into the ocean it is joined by first the Alagnak and then the Naknek River. These streams each sustain their own populations of red salmon, which mix as they arrive from ocean feeding grounds and encounter the commercial fishery in the Kvichak-Naknek district.

Note.—Approved for publication Jan. 30, 1961. Fishery Bulletin 192.

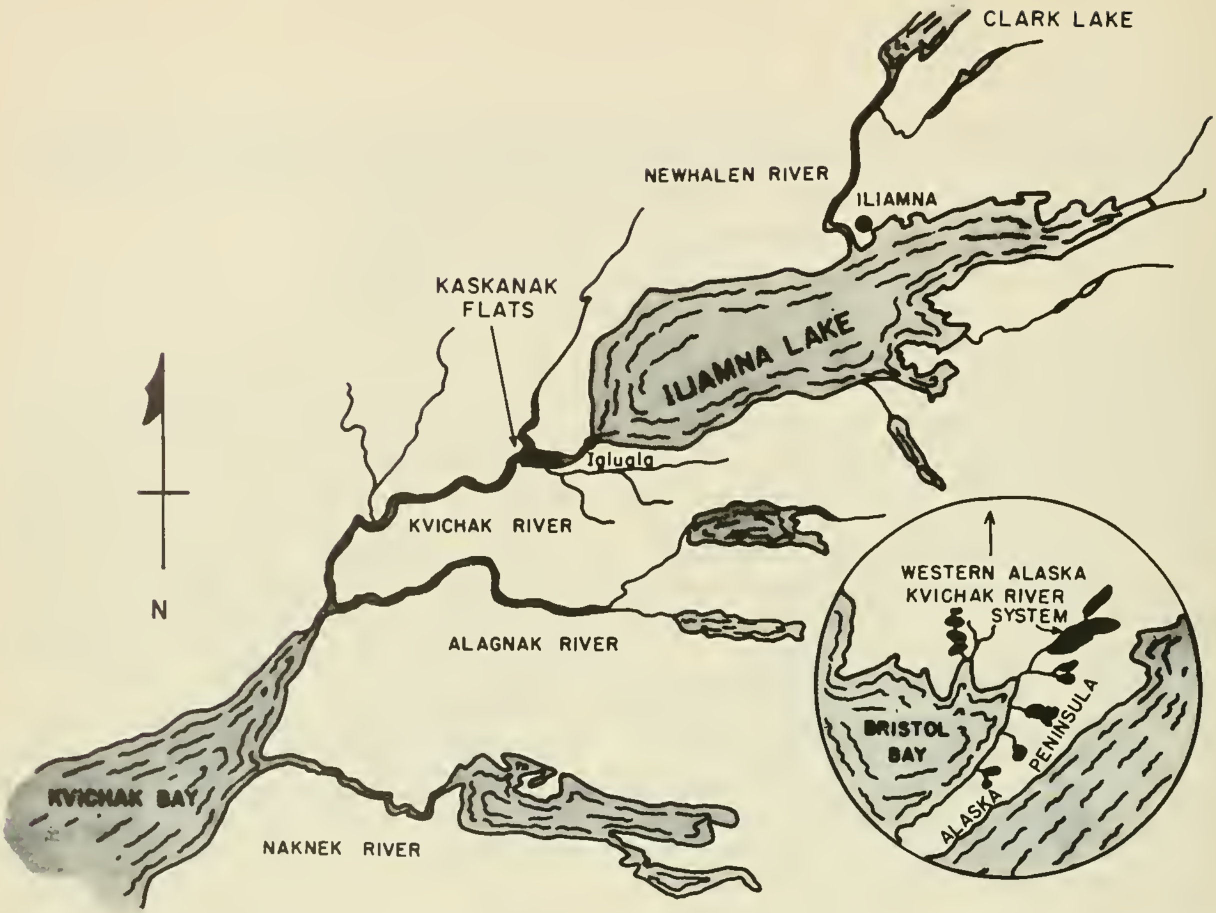

FIGURE 1.—Kvichak River system: one of the principal spawning areas for red salmon in the Bristol Bay region of western Alaska.

The Kvichak-Naknek district is one of several areas in Bristol Bay in which commerical fishing is permitted. The fishery came into large production at the turn of the century. Continuous catch and pack records since that time show tremendous fluctuations in abundance of red salmon from year to year. These fluctuations have formed a cyclic pattern with peak catches usually occurring every 4 or 5 years. From 1910 to 1958, the average annual catch was 9 million fish. The peak catch was taken in 1938 when 21 million red salmon were supplied to local canneries. Since 1938, however, the cycles tended to decline, and the catch reached a 60-year low of 923,000 fish in 1958.

Accurate estimates of escapements into the Kvichak River system are lacking for the years prior to 1955. In only one year was the entire escapement counted: in 1932, when the Bureau of Fisheries passed 5,065,000 salmon through a weir on the upper river (U.S. Bureau of Fisheries, 1933). Continued enumeration by weirs proved impractical because of excessive costs of construction and maintenance, hence, their use was discontinued.

Catches have been used in some areas as indices to escapements. But catches in the Kvichak-Naknek district include fish destined for the Kvichak, Naknek, and Alagnak Rivers, and to a lesser extent, the Egegik River. In addition, yearly changes in the distribution of gear, the intensity of the fishery, and contributions of the various runs, all vary the relation between catch and escapement. For these reasons, the catches are poor indices to red salmon escapements up the Kvichak River.

Estimates of the numbers of salmon on the spawning grounds, obtained from aerial surveys, have also been used as means of determining the escapements. However, detailed surveys of the numerous and widely distributed spawning areas of Iliamna Lake in the past 5 years have failed to reveal more than 20 percent of the estimated total Kvichak migration as determined from observation-tower counts. This percentage has varied from year to year; also the relative number of total spawners in each major spawning area has varied from year to year, irrespective of the size of the escapement. Hence, indices based on counts of spawning fish in the Kvichak River system appear to be highly unreliable.

METHOD OF OBSERVATION

The sample-count method of estimating escapements is based on the migratory habits of red salmon as they move up the river toward the area in which they originated. Salmon first appear in the Kvichak River the latter part of June and continue to pass upriver throughout July, with a migration peak occurring near the middle of the month. Once in the river the fish seek places where currents are reduced. Since areas of low currents are usually found near the bottom and next to the banks, the migrants follow restricted paths close to the shore where they can be readily observed. This habit is quite consistent in sections above tidewater where the river is confined to a single channel and where there are swift midstream currents.

It has been found that current velocities 6 inches from the bottom at the sites where the counts are taken range from 1.55 to 2.13 ft. a second, while those 6 inches from the surface range from 2.34 to 3.34 ft. a second. In 1959, the migrants passed upriver at an average relative speed of 1.52 ft. a second against the bottom currents.

Varying water levels influence the paths taken by the fish. Red salmon generally follow the banks more closely when the water level is high because of the relatively greater area of deep and quiet water close to shore. Kvichak water levels at the first of July have varied more than 2 feet from year to year, and usually rise from 8 to 14 inches during that month.

Fish appear in small separate schools when the size of the run is low. As the magnitude increases, the schools become larger and extend until the fish are passing in continuous bands. The separate schools behave somewhat erratically, but when the migration intensity is high the fish are less wary and follow the banks more closely. The direction of migration is usually continuously upriver. Only a few fish return downstream at the Kvichak counting site, and these occur invariably near the end of the migration. Slack water areas and sloughs are utilized by some individuals to rest. These fish commonly bear injuries from gill nets and predators in the ocean.

From extensive beach seining the Kvichak River escapements have been found to consist almost entirely of red salmon. Other species of salmon occur in the seine samples largely near the end of the migration, and make up less than 0.5 percent of the total escapements. The other species are omitted from the counts when identified from the towers, and therefore the possible error caused by including species other than red salmon is very small.

The visual counts are taken from towers erected at suitable locations, aided by use of background panels to silhouette the fish, turbulence reducers to smooth the surface, and other special counting aids. Once all migration paths can be observed clearly, it is relatively simple to count during sampling periods of predetermined length and to estimate the total escapement with a high degree of accuracy.

Tower Locations

The migratory habits of the fish and the physical characteristics of the Kvichak River limit the number of suitable sites for observation towers. The river below Kaskanak Flats is turbid and subject to tides that periodically reverse current flow. Migrants filter through the channels of the flats in numerous locations. Consequently, the most practical counting sites are limited to the area above the flats. The counting sites selected are near the outlet of Iliamna Lake close to the village of Igiugig and more than 50 miles upriver (fig. 1).

For peak efficiency, towers should be located where the moving bands of fish are constricted in width and pass without deviating from near the base of the structures. Since the river near Igiugig is split by an island, three towers are required (fig. 2). Towers No. 1 and No. 2 provide for sampling of the two primary paths in the main channel, which has a width of 380 feet and a maximum depth of about 16 feet. Tower No. 3

covers a shallow secondary channel through which the fish migrate when the water level is high. No fish passed through this secondary channel in 1957 and 1959 because of low water levels. The heaviest runs generally pass at tower No. 1 where a steep gradient and swift midstream currents tend to hold the salmon inshore where they pass in a narrow band. At tower No. 2, the gradient is more moderate and currents are reduced. Consequently, the fish spread over a broader area, particularly after the tower has been erected.

Tower No. 1 was constructed from spruce timbers on the right (west) bank of the river. Tower No. 2 was afloat, constructed of aluminum scaffolding and assembled on two skiffs which were lashed together and anchored off the right side of an island and on the left (east) side of the river (fig. 3). Tower No. 3 was also of aluminum scaffolding, and was located on the left (east) bank where the entire secondary channel could be observed.

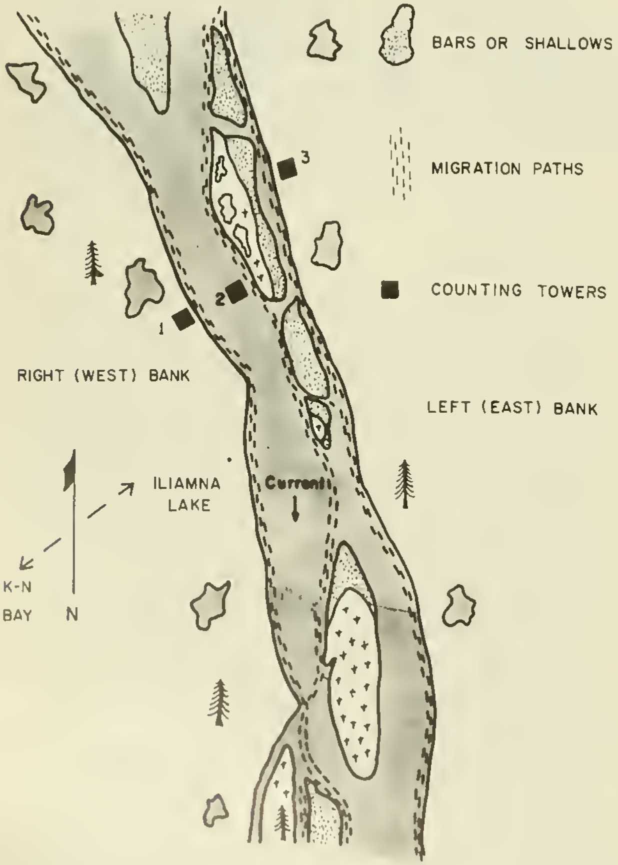

Figure 2.—Tower sites and paths of migrating fish on the Kvichak River, near Igiugig.

During sunny, calm days when the water is clear, salmon can be seen at any point in the river between towers No. 1 and No. 2. Only occasionally have they been seen near the middle and then never in a migrating band. Hence, we are confident that the salmon seen near the towers represent closely the entire migration passing at a given time.

Background Panels

Since fish blend with bottom contours making accurate counting difficult, panels were installed on the river bottom at the towers to silhouette the salmon passing. The blending is particularly camouflaging under conditions of semiturbid waters, overcast skies, and distorted river surfaces. The panels were painted a light gray to make the salmon visible under all but the most adverse conditions. As a rule, the fish will pass readily over any panel of dark or dull tones in preference to panels of bright tones. Such panels are particularly important for counting fish at night when artificial lights must be used.

In addition to revealing fish, panels must not startle the migrants, must be easy to install, and must resist deterioration in the current. Panels of 16-gage woven-wire screen of ¼-inch mesh have proved satisfactory. These panels are 3 feet wide, 10 feet long, and reinforced along the edges by 1-inch iron pipe (fig. 4). When placed in position, the panels extend out and downstream across the migration paths. Stakes of ¼-inch iron pipe, 18 inches long, are driven through metal loops to hold the panels in position.

Turbulence Reducers

Surface distortions resulting from rain, wind, waves, and bottom contours detract from accuracy of counting by reducing visibility. Turbulence reducers, an arrangement of boards and logs utilized to eliminate surging currents and wave action (fig. 5), are used to smooth the surface of the water over the panels so that the migrants can be readily seen. The wooden float is on the surface of the river immediately upstream from the panels and should not startle the fish by bobbing in the current or with vibrating anchor lines. Normally 4 feet of water is necessary before fish pass underneath undisturbed.

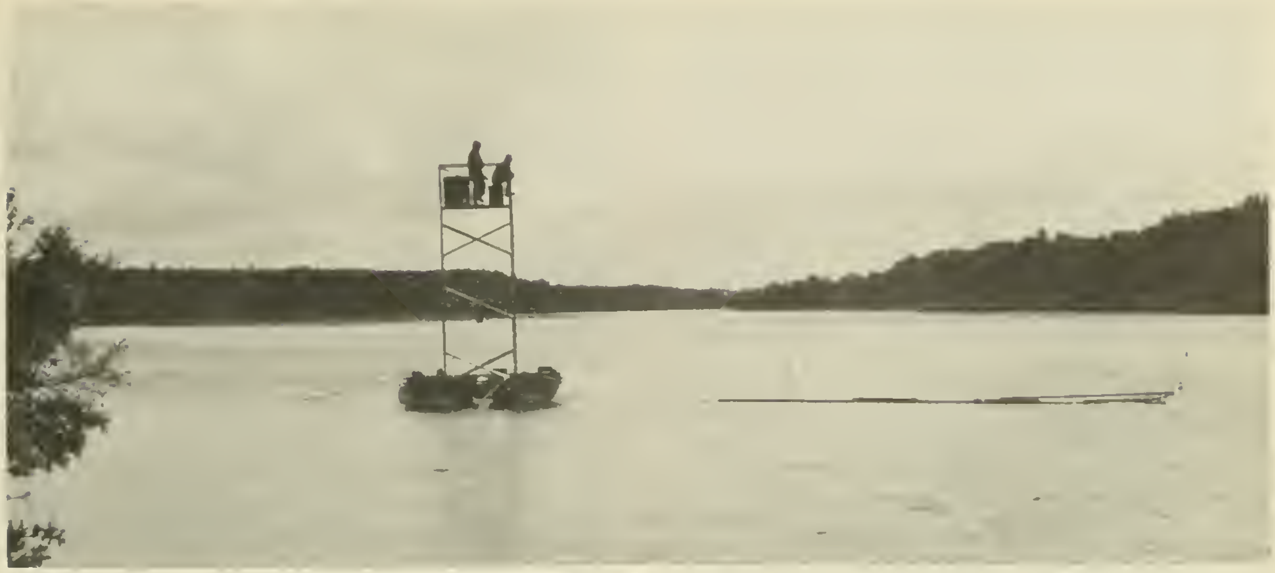

FIGURE 3.—Tower No. 2, the floating tower from which migrating red salmon were counted on the Kvichak River.

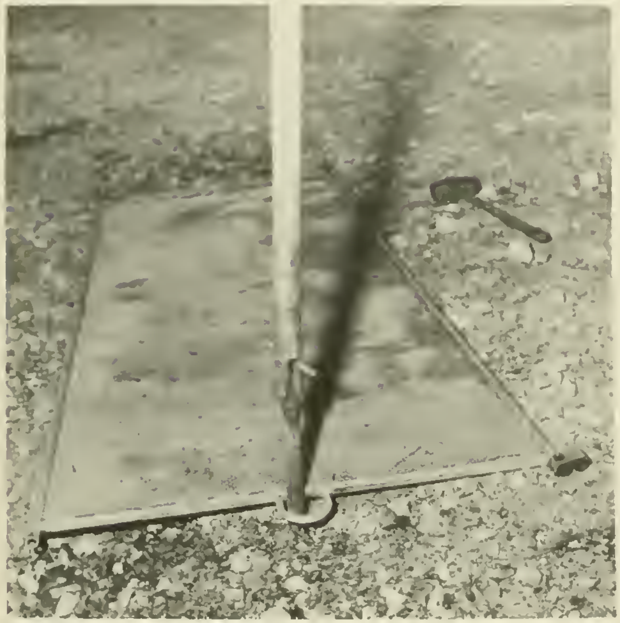

FIGURE 4.—Background panel used on river bottom to silhouette passing fish. Pin and driving rod in foreground. (Photograph by E. F. Marten.)

Three types of turbulence reducers have been used. The simplest was a log placed diagonally across the current. The second was a large V-frame, constructed from two or more timbers and placed with the apex upstream. The third and most efficient was a modification of the second, in which the effectiveness was increased by adding vertical pickets about 18 inches long and 3 inches apart to straighten subsurface currents. The latter type was originally developed and tested by the Fish and Wildlife Service on the Naknek River in 1957.

Experiments to improve visibility have also been conducted with a transparent plastic sheet which trailed on the surface of the water. The sheet smoothed the surface and did not disturb the migrants under moderate weather conditions, but rain, winds, and waves destroyed its effectiveness.

Counting Aids

Accuracy of counts was further increased by the use of (1) Polaroid glasses to reduce sun glare and surface reflection, (2) hand tallies to record

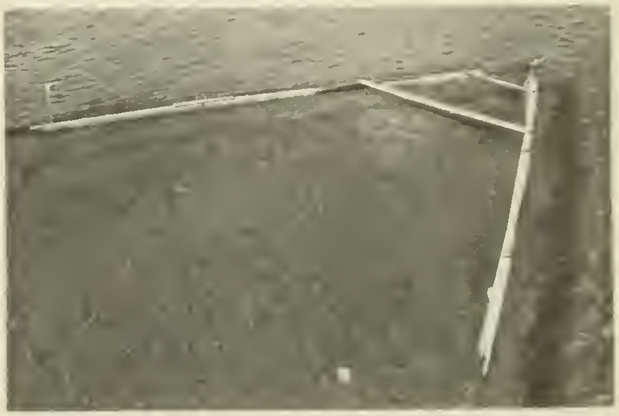

FIGURE 5.—A large turbulence reducer without vertical pickets smoothing an area 40 feet wide.

the migrants quickly and efficiently, (3) audible timers to limit the counting periods precisely and eliminate the need of watching a clock, (4) guiding devices to lead the migrants over the panels, and (5) spotlights to assist in night counts.

ESTIMATION OF THE RUNS

The sampling procedure was designed to obtain a reasonably accurate estimate of the total escapement while staying within the limits of both manpower and budget. Most of the information on which the initial sampling plan was formulated was known from previous observations of red salmon moving upriver and through weirs. Usually the major peak of the migration occurred in a day or two, although it was often preceded or followed by minor peaks. There were usually marked variations in numbers of fish from day to day and throughout a given day. In some locations near the fishery there were also marked changes in the numbers with the opening and closing of the fishing periods or with changing tides. It has since been noted at Igiugig on the Kvichak River that the heaviest runs usually appear along one bank at a time, with comparatively small numbers of fish passing along the opposite shore. The major path of the run changes erratically during the season and from year to year, but once a heavy run develops along one bank, it is usually maintained for several days.

A typical migration up the Kvichak River was counted continuously on July 16, 1955, in front of tower No. 1 (fig. 6). The fluctuations during daylight ranged from about two-thirds of the mean of 507 fish each 10 minutes to about one and one-half times the mean. With such variations, it is desirable to sample every day and within each day to use a large number of short counting periods equally spaced in a systematic fashion.

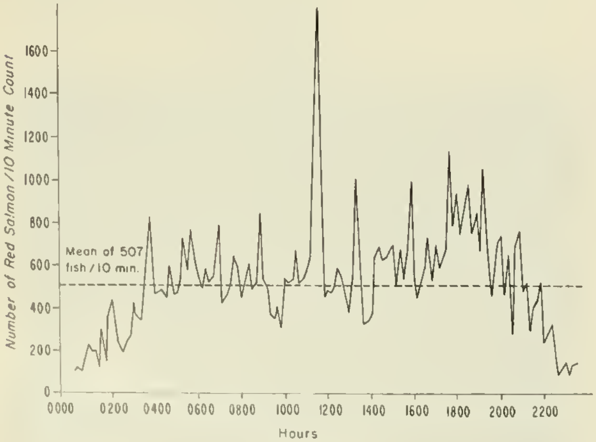

FIGURE 6.—Numerical fluctuations in migrating red salmon, from 10-minute continuous counts taken on July 16, 1955, at tower No. 1.

Since the magnitude of the escapement fluctuates greatly, even in successive 10-minute counts, the estimates calculated from the samples are basically point estimates. A single count depicts accurately only the number of fish that happens to be passing at the time. Frequent counts depict accurately only the number of fish passing when the counts were taken, yet they are closely related to the total numbers in the fluctuating population. As a result, the daily estimates obtained from the counts approximate the numbers of migrating salmon, with the accuracy depending on the magnitude and frequency of the fluctuations and the frequency and duration of the sample counts.

Method of Sampling

The basic sample unit used in 1957, 1958, and 1959 consisted of 10-minute counts taken systematically each hour from each tower. The initial sample counts in 1955 were of 2 hours' duration and taken every 4 hours. In 1956, counts were eventually reduced to 40 minutes and were taken every 3 hours. But the 10-minute counts were found most practical to obtain and to use in calculating the estimate. Any sampling procedure will be improved if it is flexible enough to permit increases or decreases in the degree of coverage with the intensity of the migration. Consequently, at the beginning and end of the migration the counts were taken every 2, 3, or 4 hours. Also, at the peak of the migration or if a heavy run commenced along one bank, counts were increased to 15 or 20 minutes. This flexibility placed emphasis on increasing the accuracy of the total estimates by concentrating the counts on the periods with the heaviest escapements.

Counts were taken by natural light as early in the morning and as late at night as possible. The hours of darkness normally extend from 2300 to 0200, but often vary from day to day depending on the extent of sky overcast and the season. Accurate night counts depend on seeing the fish by means of artificial light from spotlamps. The intensity of these lamps was controlled by a rheostat; however, when the lights were sufficiently dimmed so that the salmon passed without hesitation, the counts were not so accurate as desired. Consequently, night counts were taken from only one tower in 1957 and not at all in 1958. In 1959, night counts were successfully obtained throughout the season by using a single, bright spotlight focused outside of the panels from the top of the towers. The fish passed in the dim area inshore from the spotlight and could be seen satisfactorily when crossing the background panels. Amber and red lenses were used experimentally in 1957 to determine whether the salmon would tolerate high illumination intensities when the lights were colored. The colored lights caused stronger avoidance reactions than dimmed white lights, and also were less penetrating in waters that were moderately turbid.

The tallying procedure varied with the intensity of the migration. Fish can be tallied separately when the number passing is fewer than 250 per minute. After the run exceeds this quantity, fish must be tallied by estimating groups of 10. Heavy runs requiring such grouped counts occurred only near the peaks of the larger escapements, such as the ones that occurred in 1956 and 1957.

Method of Calculation

The calculating procedure for estimating numbers of red salmon utilized the sample count as an estimator of the number of fish passing in a given unit of time. Therefore, with 10-minute counts taken hourly, the estimate of numbers of fish passing a tower is the product of multiplying the count by six. Daily estimates are the sum of calculated hourly estimates for all towers, and the seasonal estimate is the sum of all daily estimates.

Whenever systematic counts ceased at night or when the waters were turbid with sediment, the number of fish passing has been determined by averaging the counts preceding and following the periods with no counts. The estimate has been calculated by multiplying this average by the appropriate time factor.

Results

Estimates for Kvichak River escapements have varied widely from year to year, as would be expected from the cyclic nature of the runs and the changing intensities of the commercial fishery. These totals for the past 5 years were: 250,546 in 1955; 9,443,318 in 1956; 2,842,810 in 1957; 534,785 in 1958; and 680,000 in 1959.

TABLE 1.—*Kvichak daily estimates of red salmon escapements, 1955 through 1959*

Date	1955	1956	1957	1958	1959
June 21					308
22					623
23	120	8		0	307
24	256	38		0	99
25	509	32		0	212
26	166	30	7,337	24	914
27	211	88	4,987	29	416
28	38	263	2,922	58	1,133
29	90	229	9,305	515	440
30	112	343	55,827	582	1,098
July 1	186	311	51,797	174	588
2	148	311	62,332	1,485	384
3	102	373	82,789	960	1,152
4	151	11,280	60,394	153	7,872
5	3,426	10,256	70,371	129	49,612
6	24,364	63,065	48,245	48	51,288
7	9,125	75,851	45,703	29,328	48,780
8	657	134,163	83,275	161,109	30,758
9	893	221,055	56,435	148,760	12,524
10	918	268,179	133,815	44,945	19,097
11	12,766	268,048	269,310	24,802	32,627
12	11,351	375,393	358,194	3,575	21,285
13	6,937	498,944	461,961	2,241	52,818
14	5,458	583,882	371,154	3,966	88,226
15	21,578	694,874	147,430	43,458	90,994
16	73,304	923,007	88,426	47,559	55,343
17	31,822	1,053,583	56,012	5,946	23,398
18	13,398	910,574	30,330	1,530	16,093
19	5,726	711,050	49,258	879	17,357
20	4,146	650,430	72,705	1,017	13,225
21	4,781	606,643	37,966	2,673	9,140
22	4,537	440,420	26,820	834	5,637
23	3,972	288,795	23,152	2,130	5,631
24	2,245	212,571	25,612	2,274	3,801
25	2,187	154,609	14,537	999	1,514
26	1,073	98,495	[1] 34,409	357	2,119
27	962	66,923		543	2,189
28	785	37,516		938	2,592
29	797	25,100		384	1,800
30	545	20,353		381	390
31	409	15,999			[2] 6,216
Aug. 1	213	14,558			
2	82	5,676			
Total	250,546	9,443,318	2,842,810	534,785	680,000

[1] Estimate for July 26, 27, and 28 based on irregular daytime samples.
[2] Estimated late season migration.

Daily estimates for these years are listed in table 1, and a graphic comparison of the daily escapements thus obtained is presented in figure 7. The escapement of 1956 was the largest red salmon run ever counted moving upriver in Alaska. The escapement of 1955 undoubtedly was one of the smallest noted in the history of the Kvichak River system.

The significant part of the Kvichak River escapement has always passed the Igiugig towers within approximately 3 weeks (table 2). The peak varied from July 8–9 in 1958 to as late as July 17 in 1956. The end of the runs, defined as the points where the daily escapements are less than 1 percent of the final total, are relatively unimportant to the total estimates. Small numbers of fish usually continue upriver even after the counts are terminated. Earlier, before the counts commence in the

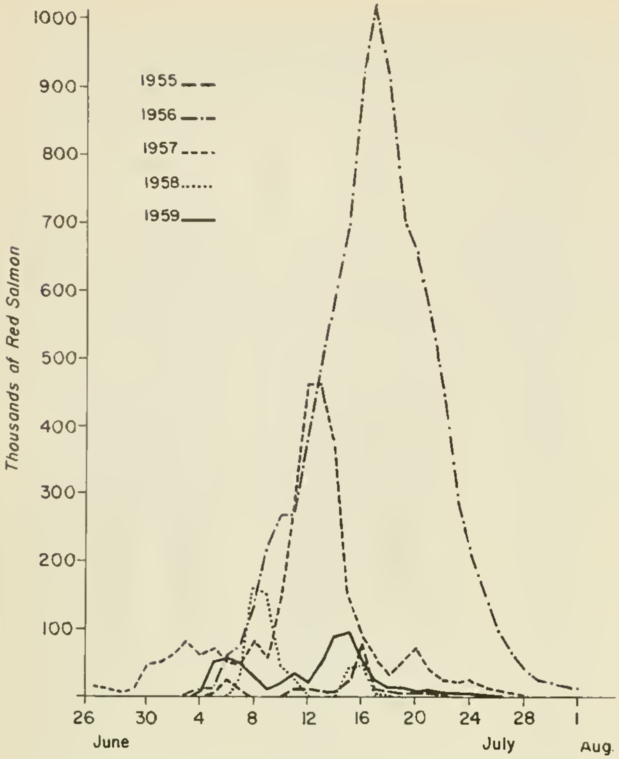

FIGURE 7.—Daily escapements of red salmon up the Kvichak River, 1955 through 1959.

spring, a few fish migrate upriver; adult red salmon have been reported taken in gill nets on upper Iliamna Lake as early as June 6.

There has been no apparent correlation between the duration and the size of the escapements. The main part of the small 1955 and the large 1956 escapements each passed in 19 days, and neither the start nor the end of the migration in the 2 years was more than 3 days apart.

FACTORS INFLUENCING VISUAL COUNTS

To a large extent, the accuracy of the basic sample counts depends on (1) individual counters, (2) migration intensity, (3) weather conditions, and (4) disrupted migration patterns. Once the relationships of these factors to the counts are recognized and understood, they can be taken into consideration in improving the counting method.

Errors Introduced by Individual Counters

Counting errors are known to result from individual differences in seeing, counting, and recording numbers of passing salmon. In 1957, 32 counts of 5 minutes' duration were taken by 2 observers counting simultaneously from the same tower. One counter (A) participated in all counts, while the other counter was taken from a group of three men designated XYZ. The data obtained are listed in table 3, where the difference in numbers of fish counted by XYZ is expressed as a plus or minus percentage of variation from A's count.

The range of variations between the 5-minute counts of A and one of the other three counters extends from −22.1 to +17.9 percent. By combining two consecutive counts to form standard 10-minute counts, the range is shortened from −7.8 to +10.7 percent. Further reductions occur when the counts are totaled and the differences calculated. For the two groups of 5-minute counts, the total differences are but +3.5 and −5.3 percent, respectively. The totals of all 32 counts differ by only −1.0 percent. Consequently, errors occurring in counts between paired observers, operating under a variety of observation conditions, tended to cancel out. Such counting errors, therefore, apparently occurred randomly and probably did not bias estimates of the escapement.

TABLE 2.—*Size and timing of Kvichak red salmon escapements at Igiugig, 1955 through 1959*

Year	Size of escapement	Timing of 95 percent of the escapement			
		Start	Peak	Stop	Range (days)
1955	250, 546	July 5	July 16	July 23	19
1956	9, 443, 318	July 8	July 16–18	July 26	19
1957	2, 842, 810	June 30	July 12–14	July 21	22
1958	534, 785	July 7	July 8–9	July 17	11
1959	680, 000	July 4	July 14–15	July 23	20

Errors Associated With Migration Intensity

As intensity of the migration increases, fish must be tallied more rapidly. An increase in migration intensity might indicate an increase in counting errors. The comparative data (fig. 8), however, show only a slight correlation between migration intensity and percentage of counting variation, even though greater variations in total numbers of fish counted did occur. This indicates that counts taken during increasingly heavy runs do not necessarily inject an increasing number of errors into the calculations.

The five comparative counts with extreme variations exceeding a plus or minus 10 percent ap-

TABLE 3.—*Comparison of counts during the same period by different observers*

1957	Tower No.	Time	Number of fish counted						Percentage variation		
			Counter A			Counters XYZ			5 min.	5 min.	10 min. (total)
			5 min.	5 min.	10 min. (total)	5 min.	5 min.	10 min. (total)			
July 9	1		63	9	72	66	9	75	+4.8	0.0	+4.2
11	1	1900		228	228		212	212		−7.0	−7.0
	2	1915	1,020	860	1,880	1,100	880	1,980	+7.8	+2.3	+5.3
12	1	1500	631	680	1,311	720	700	1,420	+11.0	+2.9	+8.3
	2	1515	700	600	1,300	650	620	1,270	−7.1	+3.3	−2.3
	1	0715	306	659	965	327	574	901	+6.9	−12.9	−6.6
13	2	1020	960	950	1,910	1,020	740	1,760	+6.3	−22.1	−7.8
14	1	0900	688	745	1,433	658	703	1,361	−4.4	−5.6	−5.1
	2	0915	487	510	997	574	530	1,104	+17.9	+3.9	+10.7
	1	1700	760	653	1,413	755	560	1,315	−0.7	−14.2	−6.9
	2	1715	413	440	853	395	443	838	−4.4	−0.7	−1.7
15	1	1900	93	76	169	92	75	167	−1.1	−1.3	−1.2
	2	1915	280	285	565	276	285	561	−1.4	0.0	−0.7
16	1	1700		70	70		67	67		−4.3	−4.3
	2	1715	190	94	284	190	98	288	0.0	+4.3	+1.4
17	1	1700	36	50	86	34	48	82	−5.6	−4.0	−4.7
	2	1715	18	106	124	18	99	117	0.0	−6.6	−5.6
Total			6,645	7,015	13,660	6,875	6,643	13,518	+3.5	−5.3	−1.0

peared when the migration passed 450 fish per 5-minute interval, but even these errors followed a random pattern and tended to average out. However, because of the greater magnitude and importance of these errors, it is imperative to increase the number of samples taken with an increase in intensity of the run. This greatly increases the reliability of the calculated estimates.

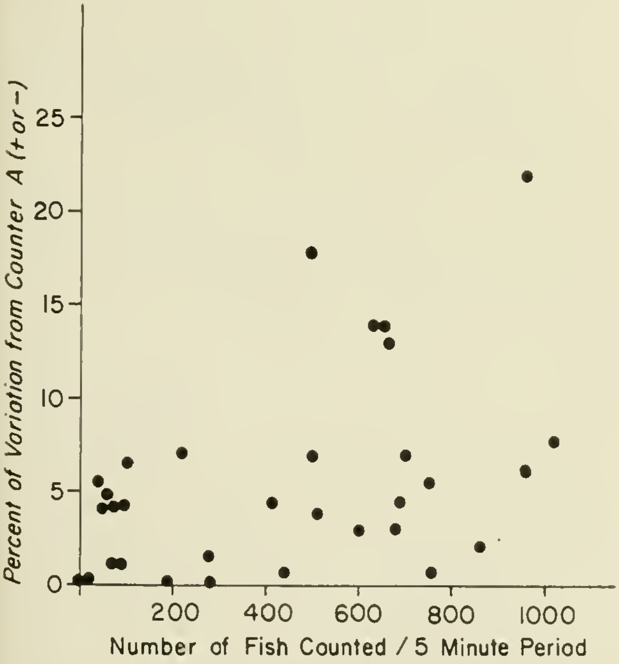

FIGURE. 8.—Relation between migration intensity and variations between counters.

When extremely heavy runs occur and samples must be obtained by estimating groups of 10 fish, counting errors are undoubtedly greater than when individual fish can be tallied. Heavy runs requiring such counting procedures are infrequent and usually occur past one tower at a time. On the Kvichak River, such runs appeared only during the intense 1956 escapement (July 11–21) and briefly in 1957 (July 12–14).

Effect of Weather Conditions

Sun glare, overcast skies, wind, and rain lower visibility and increase the difficulties of obtaining accurate sample counts. Glare may be troublesome during a 4-hour period daily when the sun is bright and low over the water. Overcast skies impart a dull appearance to the surface of the water, while upriver winds and rain disturb the surface and thereby distort the outlines of objects under the surface. The effects of these adverse conditions, combined with the normally turbulent water surface, make turbulence reducers essential. Then, with the aid of Polaroid glasses, the observers can count the passing fish accurately at almost any part of a given day.

Moderately turbid water, which occurs irregularly throughout the season, is the most important factor affecting the accuracy of the counts. This turbidity is the result of heavy breakers against the beach at the outlet of Iliamna Lake, which occur with strong east winds. The pounding causes excessive amounts of silt to be suspended in the water which then flows downriver and reduces visibility at the tower sites. Occasionally the point is reached where counts are not possible. This is discussed as high turbidity, under the section on "Accuracy of the Estimates."

When the water is moderately turbid, the variation between comparative counts might be expected to increase. Yet the data presented in table 4 show that the variation between comparative counts taken in moderately turbid water was less (+1.7 percent) than those obtained in clear water (−3.0 percent). This suggests that moderately turbid water did not increase the counting variation between two counters. It does not indicate that both counts were as accurate in turbid water as in clear water, especially on the fringe areas of the migration paths.

Effect of Disrupted Migration Pattern

Migration past a tower is momentarily disrupted as the fish scatter into deep water when the skiff bearing the counter arrives. While the fish soon re-form their ranks and resume an apparently normal migration pattern, it is possible that commencing the counts as soon as the counter is ready would inject directional errors.

A test of the timing of the counts to the time of the counter's arrival was made in 1957 by comparing the first and second 5-minute counts of 841 samples (table 5). In most instances these counts were started as soon as the counter had tied the skiff, climbed the tower, and readied his equipment, a period of 1 or 2 minutes. Since the first count was higher than the second almost one-half the time, i.e., neither consistently higher nor lower, the counts were probably not biased. The time required in preparation to commence the counts, therefore, is evidently sufficient for the migration to assume a normal pattern.

TABLE 4.—*Effect of turbid water on count variation*

Counter	Number of fish counted in—					
	Clear water			Moderately turbid water		
	1st 5 minutes	2d 5 minutes	Total	1st 5 minutes	2d 5 minutes	Total
A	3,988	3,988	7,976	2,657	3,027	5,684
XYZ	4,078	3,658	7,735	2,797	2,986	5,783
Percent variation	+1.3	−8.1	−3.0	+5.3	−1.4	+1.7

ACCURACY OF ESTIMATES

Estimates of the total migration are subject to statistical error because of periods when the continuity of the sample counts is interrupted, and because of fluctuations in abundance of fish from one counting period to another. At present we can only guess at possible bias that may accrue because of interruptions in the counts, but we can estimate precisely the possible statistical error for fluctuations of abundance. For example, it is possible to calculate confidence limits for each annual escapement to determine the reliability of the sampling program. In addition, various mathematical tests can be applied to determine the effects of changes in the length of the samples and the interspacing periods.

Effect of Interruptions in the Counts

Interruptions in counting have occurred because of high turbidity when no fish can be seen, also because of darkness, especially before satisfactory lighting was developed.

Highly turbid water occurred 10.9, 3.7, 3.1, 6.2, and 5.5 percent of the time in the years from 1955 to 1959, respectively. Once the river becomes turbid it normally remains in that condition for at least 24 hours, because the water takes about 8 hours to clear after the east wind ceases. The periods when high turbidity prevailed, in relation to the magnitude of the escapement each year, are shown in figure 9. Only in 1957 did the water turn highly turbid when a heavy migration of red salmon was passing the towers.

Beach seine hauls have been obtained occasionally to provide relative indications of migration intensity in turbid waters. These hauls are probably more effective in turbid than in clear water because of inability of the fish to see the net. Yet, catches were low, indicating a low migration intensity. A systematic comparison of hauls in clear and in turbid water was made in 1958, where the average catch per haul along the right bank was compared with the estimated number of fish migrating past tower No. 1 (fig. 10). The curve formed by this relationship indicated that few fish were migrating in the highly turbid water. Therefore, calculations of the migration for the period of turbid water, based on an average of low counts immediately preceding and following the turbid period, were basically correct.

TABLE 5.—*Relation of 1st 5-minute counts to 2d 5-minute counts, Kvichak River, 1957*

Category	Counter									Total
	A	B	C	D	E	F	G	H	I	
1st count (high)	56	83	54	88	42	57	6	5	26	417
2d count (high)	43	82	46	89	49	61	8	10	36	424
Number times counted	99	165	100	177	91	118	14	15	62	841
Percent 1st count high	56.6	50.3	54.0	49.7	46.2	48.3	42.9	33.3	41.9	49.6

Night counts were not taken in 1958 because of difficulty in counting the fish and the questionable accuracy of counts made under floodlights. Instead, estimates were made on the assumption that the migration was constant between the last evening count and the first morning count. The total time lost to sampling by omitting night counts each day was 4 hours, 2300—0200. Estimates of the escapements based on systematic night counts in 1957 and 1959 from tower No. 1 were compared with those calculated by averaging the 2200 and 0300 samples (table 6). In both instances the escapements test-calculated by omitting night counts were high, 6.8 percent for the larger 1957 run and 34.6 percent for the smaller 1959 run. Consequently, it is necessary to obtain night counts whenever possible to maintain a high degree of accuracy in the estimates.

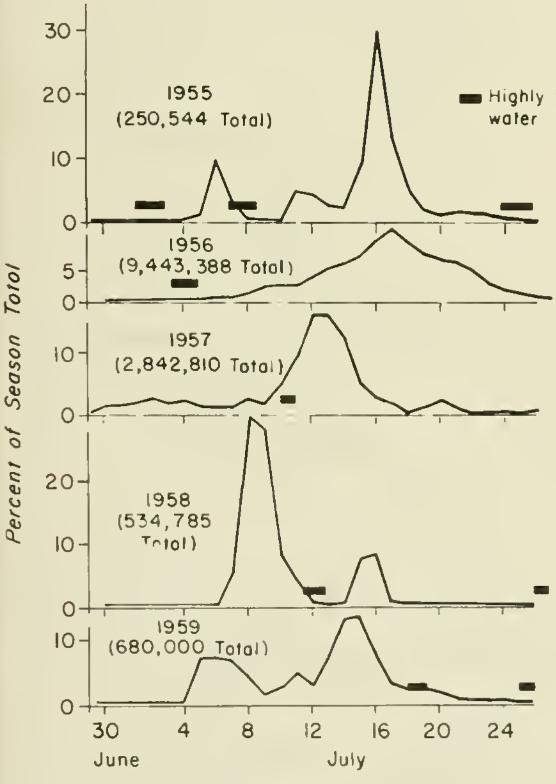

FIGURE 9.—Relationship of periods of high turbidity to red salmon escapements, Kvichak River, 1955 through 1959.

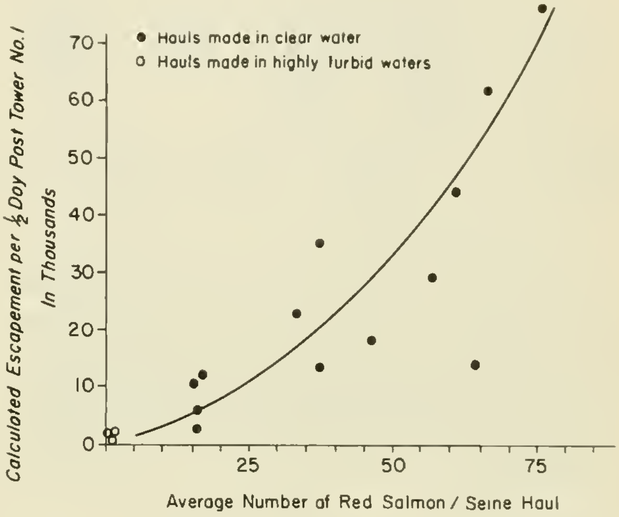

FIGURE 10.—Relation between average numbers of red salmon caught per seine haul and the calculated number of fish passing tower No. 1. Data computed on a ½-day basis, Kvichak River, July 7–17, 1958.

Population Fluctuations

Fluctuations in numbers of migrating fish from season to season, from day to day, and from hour to hour, are characteristic of Kvichak River salmon runs. Seasonally, the fluctuations have ranged from ¼ to 9½ million fish. Daily fluctuations were clearly defined in small escapements, less defined in large runs.

However, fluctuations taking place between counts are of the greatest importance to the estimates of the escapement. The greater the frequency and magnitude of fluctuations from one sample to the next, the more the calculated estimates are likely to deviate from the true population passing upriver. Fluctuations from sample to sample and between samples are the result, to a large extent, of the schooling habits of the fish. These schools are particularly noticeable when the migration intensity is low, but even during a heavy run wide fluctuations in numbers continue to occur.

TABLE 6.—*Determination of possible error from omitting all night counts from tower No. 1, 1957 and 1959*

Year	Night estimate		Percentage error by method B	Percentage error in daily estimates
	A. By expanding hourly samples (used)	B. By averaging 2200 and 0300 samples (tested)		
1957	198,441	211,944	+6.8	+1.4
1959	51,454	69,240	+34.6	+6.9
Total	249,895	281,184	+12.5	+2.5

The width of the confidence intervals associated with a point estimate is influenced directly by the fluctuations in numbers of fish. The width of such intervals can be decreased by an increase in sampling time, especially by increasing the number of samples but also by expanding the length of the sample unit.

Confidence Limits of the 1959 Escapement

Confidence limits were determined for point estimates of the annual red salmon escapements.[1] The method was applied to the 1959 counts to illustrate the procedures and to point out the accuracy achieved by the present sampling methods. The counts were of 15 minutes' duration and were taken every 4 hours early in the season. A change to 10-minute counts taken hourly was made on June 29 as the migration increased. Daytime counts were increased to 15 minutes, some to 30 minutes or more each hour, near the peaks of the escapement. Then all counts were reduced to 10 minutes and taken every 4 hours near the end of the run.

Before confidence limits can be calculated, the season must first be stratified, since the variance in the counts is associated with the mean numbers of fish for each segment of the escapement (table 7). The total migration season from which the four strata were drawn extended from noon, June 21 to August 1, a total of 39.5 days. This is equivalent to 79 days of total counting for the two towers. As intended by the sampling plan, an increase in the percentage of sampling time occurred with each strata in proportion to its numerical importance; 7.8, 14.1, 22.1, and 24.8 percent with strata I to IV, respectively.

It is assumed that the sample counts were taken randomly throughout each stratum regardless of some extended counts or occasional gaps and were, therefore, representative of the stratum from which they were taken. The preliminary calculations for the determination of the confidence limits are summarized in tables 7 and 8, where—

N=total number of sampling units (10-minute counts).

P=total fish passage (population).

N_i=total number of sampling units in the ith stratum.

n=total number of samples (10-minute counts) obtained.

n_i=total number of samples obtained in ith stratum.

X_{ij}=number of fish in jth sample in ith stratum.

$\bar{X}_i$=mean number of fish per sample in ith stratum from—

$$\bar{X}_i=\frac{\sum_j X_{ij}}{n_i}$$

S_i^2=variance of the samples in ith stratum from—

$$S_i^2=\frac{\sum_j X_{ij}^2-\frac{\left(\sum_j X_{ij}\right)^2}{n_i}}{n_i-1}$$

Each stratum is weighted by $W_i=\frac{N_i}{N}$. The weighted mean ($\bar{\bar{X}}$) and the associated variance $S^2_{\bar{\bar{X}}}$) are then calculated from—

$$\bar{\bar{X}}=\sum_{i=1}^{4}\bar{X}_i\cdot W_i=60.62, \text{ also}$$

$$S^2_{\bar{X}_i}=\frac{S_i^2}{n_i}\cdot\frac{N_i-n_i}{N_i},\ S^2_{\bar{\bar{X}}}=\sum W_i^2\cdot S^2_{\bar{X}_i}$$

---

[1] The principal procedures have been used previously by O. A. Mathisen in analysis of Wood River escapement estimates: A Stratified Sampling Program for Visual Tower Counting, 1957. University of Washington, Fisheries Research Institute, Seattle (Wash.). Manuscript. Modifications in this procedure for application to Kvichak River data were made with the assistance of C. O. Junge, Jr., of the Fisheries Research Institute.

TABLE 7.—*Stratification of the Kvichak escapement in 1959*

Strata	Average number fish counted[1]	Date and site of escapement in stratum	Number sampling units (N_i)	Number samples obtained (n_i)	Percent n_i
I	0–20	All units from June 21 to July 30 other than noted.	6,912	540	7.8
II	20–80	Tower No. 1: July 4, 8, 10, 12, 18, 19, 20, 21, 22. Tower No. 2: July 12, 17, 18, 21, 22.	1,872	264	14.1
III	80–220	Tower No. 1: July 6, 7, 11, 17. Tower No. 2: July 5, 6, 7, 8, 9, 10, 14, 16.	1,728	382	22.1
IV	260–500	Tower No. 1: July 5, 13, 14, 15, 16. Tower No. 2: July 15	864	214	24.8
			$N=11,376$	$n=1,400$	--------

[1] Determined as 10-minute counts for uniformity of calculation.

The final calculations of the confidence limits, with the level of significance set at 95 percent ($t=1.96$), are made from—

$$(\overline{P}, \underline{P})=N\left[\overline{\overline{X}}\pm t_{.05}\sqrt{\Sigma(W_i^2)\left(\frac{S_i^2}{n_i}\right)\left(\frac{N_i-n_i}{N_i}\right)}\right]$$

$$=11,376\left[60.62\pm 1.96\sqrt{S_{\overline{\overline{X}}}^2}\right]$$

$$=689,613\pm(11,376)(1.96)(\sqrt{1.5213})$$

$$=689,613\pm(22,297)(1.233)$$

$$=689,613\pm 27,492$$

As calculated, the 95-percent confidence limits for the 1959 Kvichak River escapement are equivalent to ±3.99 percent (±27,492) of the 689,613 estimated total fish passage (P). Such narrow limits point to the effectiveness of the sample-count estimation program in current use.

The sum of the daily estimates given in table 1 (680,000) differs slightly from the estimate calculated from the stratified data. The tabulated value is considered the best estimate, and is well within the calculated confidence limits.

Effect of Changing the Sampling Design

The length of the counting period and the frequency of the samples are the two main variables to be considered in formulating a sampling program. Increasing or decreasing either one influences the reliability of the calculated estimates.

To analyze these variables, systematic test samples were drawn from a continuous 48-hour count obtained in 1955. The lengths of the counting period of the samples tested were 10, 20, 30, 40, and 60 minutes, while the sampling frequencies were 1, 2, 3, and 4 hours. Generally, four different tests were made with each relationship: sample period length to sample frequency. Totals of the calculated estimates were then compared with the actual total for the 48-hour period, and the percentage deviation plotted in figure 11.

The percentage of error tends to drop with an increase in the length of the samples and with an increase in the frequency of the samples. Short counts, under 40 minutes in length, provide reliable calculations when taken every 1 or 2 hours, usually ranging within a plus or minus 6 percent. These counts show a much wider range of error when taken every 3 or 4 hours. This indicates that, for a specific reduction in counting time, the most consistent results would be obtained with short samples taken frequently. The 1955 and 1956 estimates, based on infrequent larger samples, may have been less accurate than those in recent years. However, in 1955, 73 percent of the escape-

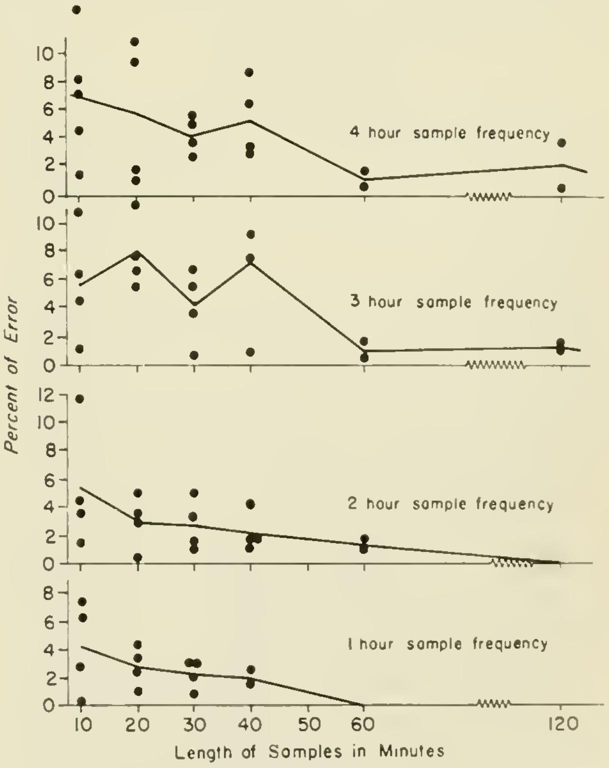

FIGURE 11.—Distribution of sampling errors with various sample period lengths and frequencies.

TABLE 8.—*Preliminary calculations for the determination of confidence limits for the 1959 Kvichak escapement*

Strata (i)	Weights		$_j\Sigma X^2_{ij}$	$_j\Sigma X_{ij}$	$\overline{X}_i$	S^2_i	$\frac{N_i-n_i}{N_i}$	n_i	$W^2_i S^2_{\overline{x}_i}$
	W_i	W^2_i							
I	0.6076	0.369,178	84,686	3,160	5.9	122.8	0.922	540	0.0774
II	.1646	.027,093	1,385,368	13.995	53.0	2,446.7	.859	264	.2157
III	.1519	.023,074	12,684,729	56,027	146.7	11,725.4	.779	382	.5524
IV	.0760	.005,776	32,187,143	73,290	342.5	33,272.4	.752	214	.6758
Total	1.0001								$S^2_{\overline{x}}=1.5213$

ment was enumerated in a continuous count. In 1956, the variation in number of fish from sample to sample was low, evidently because of the greater magnitude of the run. The basic sampling design of 10-minute counts taken hourly and supplemented by longer counts during a heavy run, therefore, appears to be highly efficient.

It is difficult to determine with any degree of precision the most efficient sampling design, since the size and nature of the migration vary from year to year. Such factors as the proper distribution of time, manpower, and equipment in obtaining accurate counts must also be considered. On the Kvichak River, short frequent counts have proved practical to obtain adequate estimates under all operating conditions.

SUMMARY

1. A method of estimating red salmon escapements by using systematic sample counts was developed and used on the Kvichak River, Alaska, from 1955 to 1959 by the Fisheries Research Institute.

2. The method was based on the fact that migrating red salmon avoid swift midstream currents and pass upriver in narrow bands close to the shores, where observation towers, background panels, turbulence reducers, and other counting aids could be used to obtain accurate counts.

3. Statistically, migrating red salmon were considered as a fluctuating finite population. The design of the sampling procedure was aimed at obtaining a reasonably accurate estimate of the total run from properly distributed visual counts throughout the migration season.

4. The basic sample unit consisted of 10-minute counts taken systematically each hour from each tower. This design was varied to provide increased or decreased coverage with the corresponding variations in the intensity of migration.

5. Estimates for a given period of time were obtained by multiplying the sample count by the appropriate factor. For longer periods when no samples were obtained, the estimates were interpolated by averaging the counts preceding and following the gap and multiplying by the appropriate time factor.

6. Daily estimates were calculated as the sum of all estimates for all towers each day, and the final escapement estimate was the sum of all daily estimates.

7. Kvichak River escapements, as estimated by the sample count method, amounted to 250,546 fish in 1955; 9,443,318 fish in 1956; 2,842,810 fish in 1957; 534,785 fish in 1958; and 680,000 fish in 1959.

8. The accuracy of each sample count was affected by different counters, migration intensities, weather conditions, and disrupted migration patterns. However, the factors were not found to inject significant directional errors but showed definite tendencies to cancel out.

9. The accuracy of the calculated estimates was affected by interruptions in the continuity of the counts from highly turbid waters and darkness and by fluctuations in numbers of fish between samples.

10. A method of determining confidence limits was illustrated. Applied to the 1959 Kvichak River escapement, the confidence limits were established at a plus or minus 3.99 percent at a 95 percent level of significance.

11. The calculated estimates were influenced by varying the lengths and frequencies of the samples. The percentage of error tended to drop with an increase in the length of the samples, and with an increase in the frequencies of the samples. Samples less than 40 minutes in length were found to provide estimates usually within a plus or minus 6 percent of error when taken every 1 or 2 hours.

LITERATURE CITED

FISHERIES RESEARCH INSTITUTE, UNIVERSITY OF WASHINGTON.

1955. How shall we defend the concept of sustained-yield conservation? Pacific Fisherman, vol. 53, No. 6, pp. 18–20.

THOMPSON, WILLIAM FRANCIS, and DAN WILEY CLANCY.

1959. Length measurement of migrating salmon by paired underwater cameras. Photogrammetric Engineering, vol. 25, No. 3, pp. 449–455. (University of Washington, College of Fisheries, Contribution No. 54.)

U.S. ARMY CORPS OF ENGINEERS.

1957. Harbors and rivers in southwestern Alaska. 89 pp., tables, charts, maps. (84th Cong., 2d sess., House document 390.) Washington, D.C.

U.S. BUREAU OF FISHERIES.

1923. Alaska fishery and fur-seal industries in 1922, by Ward T. Bower. Report of the Commissioner of Fisheries for 1923. Appendix 4. 118 pp., 16 figs., tables. (Document 951.)

U.S. BUREAU OF COMMERCIAL FISHERIES.

1956. Progress Report and Recommendations for 1957. 34 pp., 39 figs., tables. Juneau, Alaska.

1957. Progress Report and Recommendations for 1958. 26 pp., 37 figs., tables. Juneau, Alaska.

UNITED STATES DEPARTMENT OF THE INTERIOR, Stewart L. Udall, *Secretary*
FISH AND WILDLIFE SERVICE, Clarence F. Pautzke, *Commissioner*
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ATLAS OF THE OCEANOGRAPHIC CLIMATE OF THE HAWAIIAN ISLANDS REGION

BY GUNTER R. SECKEL

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ABSTRACT

In the area bounded by 10° N., 30° N., 150° W., and 180°, the distribution of surface variables is investigated in terms of associated physical processes. (1) Using all available data, seasonal changes in the distribution of the mixed surface layer, surface temperature, surface salinity, and the dynamic topography are described. (2) With the aid of a simplified heat (salt) budget, the physical processes (net heat exchange across the sea surface, evaporation minus precipitation, advection) and their relation to the distribution of surface variables are analyzed. (3) The results are interpreted in terms of a climatic circulation model in the vicinity of Hawaii.

The distribution of surface variables reveals three types of climatic boundaries: (1) a depth-of-mixed-layer boundary separating areas in which the time of maximum and minimum depths differs; (2) temperature boundary separating an area where the seasonal range of temperature is relatively constant from one in which it increases northward; (3) salinity boundary separating different types of water.

Investigation of processes reveals three cold advection periods, June-July, October-November, December-January; the first is dominant in the northwest portion of the area and the second in the southeast portion. In the course of analysis, characteristic advection diagrams, intrinsic temperatures, heat advection charts, and characteristic heating curves are defined.

In terms of the North Pacific circulation, the salinity boundary is interpreted as separating North Pacific Central water from the transition water of the California Current Extension. The June-July and October-November advection periods reflect dilations and contractions of the North Pacific Central and North Pacific Equatorial circulation systems believed to be associated with the seasonal variation of trade wind intensity. The differing times of maximum and minimum depths of the mixed layer and dominant advection periods reflect the differing climates of the North Pacific Central and North Pacific Equatorial systems.

ATLAS OF THE OCEANOGRAPHIC CLIMATE OF THE HAWAIIAN ISLANDS REGION

By GUNTER R. SECKEL, *Oceanographer*, BUREAU OF COMMERCIAL FISHERIES

A study of the oceanographic climate of the Hawaiian Islands region is a part of the Hawaii skipjack investigations conducted by the staff of the Biological Laboratory,[1] Bureau of Commercial Fisheries (Honolulu). This seasonal fishery has been described by Yamashita (1958). The catch rate generally begins to rise rapidly in April from 200,000 pounds or less a month during the winter to 2 million pounds or more in August. Thereafter it drops off rapidly in September and October, again reaching the minimum catch rate per month during the latter part of the year. The fishery also shows relatively large annual fluctuations ranging from a low of about 6 million pounds, as in 1957, to about 14 million pounds, as in 1954. Because both the seasonal nature of the fishery and its annual fluctuations were believed to be associated with changes in the physical environment, oceanographic studies were included as part of the skipjack investigations.

Oceanographic information for the waters bathing the Hawaiian Islands was summarized by Schott (1935) and Sverdrup et al. (1942), and bathythermograph observations from 1941 to 1949 were analyzed by Leipper and Anderson (1950). Since 1949, six oceanographic surveys were made in the vicinity of the high islands of the Hawaiian archipelago (McGary, 1955; Seckel, 1955). The information from these sources can be summarized as follows: The Hawaiian Islands are located in the trade wind zone of the Pacific Ocean, where seasonal changes of surface variables are relatively small. The seasonal temperature range, for example, is approximately 4° to 5° F. (2° to 3° C.). The mean summer high is about 78° F. (25.6° C.) and varies locally from 75° (23.9° C.) to 80° F. (26.7° C.). The mean winter low is about 74° F. (23.3° C.) with local variations from 73° (22.8° C.) to 76° F. (24.4° C.).

The mean salinity is about 35 °/₀₀, ranging from 34.4 to 35.3 °/₀₀. Definite seasonal salinity variations, because of insufficient data, were believed to be obscured by large annual variations.

Available surface inorganic phosphate data show that the concentration to be found in the vicinity of the Hawaiian Islands approaches the limit of precision in present experimental techniques (0.3μg-at./L.). This, together with the scarcity of observations, made it impossible to detect seasonal changes.

Zooplankton catches in the area have been discussed by King and Hida (1954, 1957) and Waldron, Nakamura, and Shippen (MS). Mean catches indicate annual variations of 15 to 25 cc. per thousand cubic meters of water strained in 200-meter oblique hauls, with a suggestion of a similar range in seasonal catch variations (King and Hida, 1957, figs. 7 and 8).

Current charts generally show a weak set toward the west throughout the year. Geostrophic currents indicate a complex flow pattern in the vicinity of the high islands, without providing any information about seasonal changes. In short, these environmental parameters are well within the limits within which skipjack are known to occur, so that their changes appear to be insufficient to explain the seasonal nature of the skipjack fishery and its annual variations.

All data, however, have not been exhausted. There are many isolated observations from cruises either originating or terminating in the Hawaiian Islands. In addition, many thousands of bathythermograph observations have been obtained by the Bureau of Commercial Fisheries Biological Laboratory (Honolulu), and other organizations since the end of World War II. These data, if treated by means of a different approach, could yield information which is not now apparent.

One can postulate, for example, that the surface variables such as temperature or salinity, are not randomly distributed in space, but that they are

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[1] Formerly Pacific Oceanic Fishery Investigations (POFI). Renamed December 1, 1959.

NOTE.—Approved for publication February 27, 1961. Fishery Bulletin 193.

associated with certain physical processes. Or, if the space and time distribution of surface variables is known, then one should be able to obtain some information about the physical processes. To be more specific, one can formulate a heat budget and say that the rate of change of heat content in the surface water (approximately proportional to the surface temperature) must depend on the rate at which heat enters or leaves across the sea surface, the diffusion (a change of concentration due to mixing), and advection (a change of concentration due to currents introducing water with different properties). Similarly, one should be able to formulate salt budgets in which evaporation and precipitation at the surface must be considered and, possibly, momentum budgets in which the surface wind stress must be considered.

Such an approach has been described in the chapter on the Theory of Distribution of Variables in the Sea, by Sverdrup et al. (1942). In practice, of course, the formulae presented there must be simplified before application. However, the equations state that whenever physical processes are to be related to the distribution of variables, such as temperature, salinity, momentum, oxygen, and phosphate, the following data must be available about the variable in question: (1) the local-time rate of change and (2) the three-dimensional space distribution. This requirement, as it concerns the heat budget of the surface water in the Hawaiian Islands region, can be satisfied by using all the available data mentioned.

In weather analysis, the seasonal changes in temperature at any location are explained in terms of solar energy received and in terms of the motions of high- and low-pressure systems. In central North America, for example, the cold, dry, winter weather is associated with the southward motion of the polar high pressure system. In summer, as this system's boundaries move northward, the cold, dry air is replaced by the maritime-tropical air moving inland through the Gulf of Mexico producing warm and highly humid weather. This type of weather analysis is called climatology and, therefore, by analogy, the investigation to be described here can be called "climatic oceanography."

In order to study the oceanographic climate of the Hawaiian Islands, the results of previous surveys (McGary, 1955; Seckel, 1955) made it evident that an area larger than the immediate vicinity of the main Hawaiian Islands must be chosen. Natural boundaries for this area, to be referred to as the Hawaiian region, are the vicinity of the northern edge of the equatorial countercurrent, or 10° N., and the vicinity of the salinity maximum, or 30° N. In the west, the 180th meridian was chosen, and in the east, lack of data limited the area to 150° W.

For this region, then, the climatic study will be divided into two parts. First, the distribution of surface parameters, such as the depth of mixed layer, temperature, salinity, and geopotential topography, will be described essentially without interpretation. Second, the processes with which these parameters are associated will be investigated. Because adequate salinity and current data are lacking, the present paper will primarily be concerned with the processes of heat exchange across the sea surface and heat advection as they are related to the distribution and rate of change of temperature throughout the region.

In the course of the analysis, "characteristic advection diagrams," "characteristic heating curves," and "intrinsic temperatures" will be defined. It will then be shown how these can be used to interpret continuous surface temperature data, such as are obtained at the Koko Head monitoring station on Oahu.

The final portion of the analysis will consist of an integrated account of the oceanographic climate of the Hawaiian Islands region. Here features of interest described in part I will, as far as is possible, be explained by the processes described in part II. Readers who are primarily interested in the results of the study can proceed directly to part III, and turn to parts I and II for details of the analysis.

The sources of data will be indicated in the Appendix, with an account of the manner in which they were treated.

Finally, the aims of the study have been achieved. Despite the fact that the data used do not readily lend themselves to an analysis of processes because they were collected for other purposes, over a period of years, at unrelated times and places, and in an area where their seasonal and annual variations are of the same order of magnitude, a gross picture of the oceanographic climate in the vicinity of Hawaii has been developed.

Although reasons for the occurrence of skipjack in Hawaiian waters are not known, the seasonal and annual variations in their abundance, as reflected by catch statistics, are associated with climatic features such as the seasonal movement of different types of water through the island area. These climatic changes can be monitored with the aid of surface temperatures and salinities as obtained at Koko Head, Oahu.

I would like to express my appreciation to the members of the faculty of the Department of Oceanography, University of Washington, for making their facilities available during a portion of the work and for providing encouragement and valuable suggestions. I would also like to thank Drs. C. A. Barnes, N. P. Fofonoff, and M. Rattray for reading the manuscript and for their valuable suggestions—T. S. Austin, J. C. Marr, and K. D. Waldron for reviewing the manuscript, Mrs. M. K. Robinson for supplying the bathythermograms from the Scripps Institution of Oceanography deck, and T. Nakata for drawing the figures and charts.

PART I. DISTRIBUTION OF SURFACE VARIABLES

1. DEPTH OF THE MIXED SURFACE LAYER

A. Definition and Practical Means of Determination

In this paper an attempt will be made to relate the space and time distribution of a surface variable, such as temperature, to physical processes such as heat exchange and advection. Although these processes will be discussed in part II, one of the parameters entering into budget considerations is the depth to which the processes at the sea surface are effective. For example, the change of temperature due to a certain amount of net heat exchange across the sea surface depends on the volume of water through which this heat has been distributed. Thus, the depth of this effective layer must be defined and its distribution must be determined.

Since the processes at the sea surface involve energy changes, it is appropriate to consider the stability generally encountered in the upper 300 meters of the Hawaii region. The stability $E=\frac{1}{\rho}\frac{\delta\rho}{dz}$ has been discussed by Sverdrup et al. (1942) and is a function of the vertical density gradient. It is also proportional to the force required to displace a parcel of water vertically by a unit length.

Figure 1 illustrates the vertical winter and summer density (σ_t) distribution at 10° N., 20° N., and 30° N., approximately along a meridian

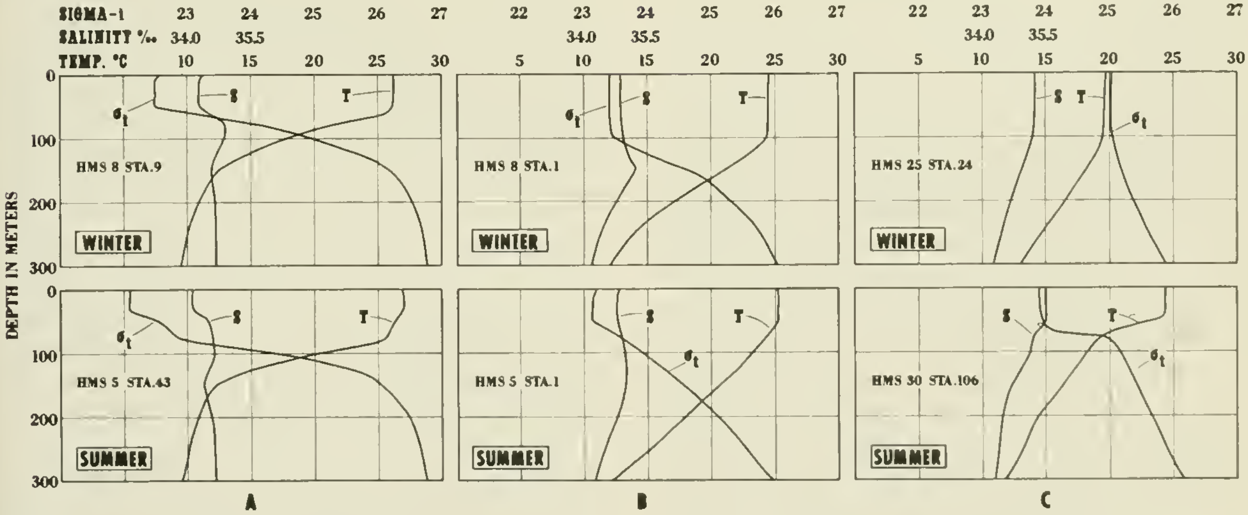

FIGURE 1.—Temperature, salinity, and density (σ_t) depth curves. Panel A, winter and summer near 10° N., 158° W.; panel B, winter and summer near 21° N., 158° W.; panel C, winter and summer 30° N., 160° W. (158° W.).

through the Hawaiian Islands. Three density layers can be readily distinguished. The first is the mixed surface layer with neutral stability $\left(\frac{\delta\rho}{dz}=0\right)$. The second, the pycnocline, is a layer within which there is a rapid increase in density with depth. The third, in which the density increases very slowly with depth, is below the pycnocline.

Approximate stabilities, $E'=10^{-3}\frac{d\sigma_t}{dz}$ (Sverdrup et al. 1942: 417), in the three layers are as follows: in the mixed surface layer $E'=0$: in the pycnocline $10^{-5}\frac{d\sigma_t}{dz}$ ranges from 3400 m.$^{-1}$ to 5000 m.$^{-1}$, 1400 m.$^{-1}$ to 2300 m.$^{-1}$, and 350 m.$^{-1}$ to 2500 m.$^{-1}$ at 10° N., 20° N., and 30° N., respectively. These compare with stabilities of 120 m.$^{-1}$ at 10° N. to 170 m.$^{-1}$ at 30° N. in the deeper layer below the pycnocline. Thus, stability changes from layer to layer are large. In addition, whereas the change from the second to the third layer is gradual, the change from neutral stability in the mixed surface layer to high stability in the pycnocline is abrupt. The bottom of the mixed surface layer can therefore be regarded as a surface of dynamic significance. Above this surface, parcels of water can move up and down with a minimum expenditure of work. In the pycnocline, a comparatively large amount of work must be done to displace water vertically. For this reason, the depth of the effective layer through which energy changes due to processes at the sea surface are distributed is assumed to be the mixed surface layer.

In order to measure the depth of the mixed surface layer and determine its distribution, it is useful to remember that the density of the surface sea water is a function of both the temperature and the salinity. These were also drawn in figure 1 to such a scale as to demonstrate their relative effect on the density. It is apparent that the vertical density structure is primarily a function of the temperature and that the salinity in the latitudes under consideration is of less importance. It is also apparent that the top of the pycnocline corresponds approximately with the top of the thermocline and that the surface layer in which $E=0$ corresponds approximately with the layer in which the vertical temperature gradient is also zero $\left(\frac{\partial\theta}{\partial z}=0\right)$. The depth of the mixed surface layer can therefore be determined from temperature-depth curves in the Hawaiian region.

In practice it is not always as simple to determine the depth of the mixed layer from the vertical temperature distribution as indicated in the examples of figure 1. It will therefore be useful to briefly review features of the vertical temperature distribution which are discussed in detail in the Application of Oceanography to Subsurface Warfare (National Defense Research Committee, 1946). The most important of these is the thermocline, in which the maximum temperature change occurs. It is between the surface layer of constant temperature and a deeper layer in which the vertical rate of change of temperature is small. In the Hawaiian region, this thermocline, which we call the main or permanent thermocline, is always present. Below the mixed layer, the average temperature gradient, $\frac{\partial\theta}{\partial z}$, is approximately 15° C., 6° C., and 5° C. per 100 m. at 10° N., at 20° N., and 30° N., respectively. Superimposed on the permanent thermocline may be a seasonal thermocline. This is illustrated by the vertical temperature distribution at about 30° N. in winter and summer (fig. 1C). In addition to the permanent and seasonal thermocline, there may be a diurnal thermocline, defined as a small rise in surface temperature of the order of 1° C., which may extend to a depth of 10 m. Finally, the stable layer may extend to the sea surface; i.e., the constant temperature surface layer may be absent.

The last two rarely occur in the area under investigation and the practical problem remains one of determining the depth of the mixed surface layer with consistency from .temperature-depth curves. In low latitudes the depth of this layer is generally well defined by what Munk and Anderson (1948) called the "knee." However, more than one knee may occur, as at 10° N. in August, illustrated in figure 1A. In examining temperature-, salinity-depth curves in the Hawaiian region, one finds that the first knee, after excluding the diurnal thermocline, also defines the layer of constant salinity, whereas deeper knees are in more saline water.

Difficulty also arises when the depth of the knee is not well defined and may actually lie within a layer of changing salinity with depth, the halocline. In other words, the temperature decreases gradually below a layer of constant temperature or below the sea surface. It is useful, then, to define a vertical temperature gradient which separates the mixed surface layer from the thermocline. A gradient of 3.6° C. per 100 m. (1° F. per 50 ft.), which apparently is of significance in connection with underwater sound properties,[2] has been used by the Scripps Institution of Oceanography. By examining temperature- and salinity-depth curves it was found that this gradient was too large and that the apparent depth of the surface layer in many cases was well within the halocline. Lumby (1956) took as the criterion for the homogeneous layer the depth of the isothermal layer as judged by the absence of temperature gradients in excess of 1° C. per 100 m. Upon examination, it was found that the apparent depth of the mixed layer, using Lumby's criterion, was in good agreement with the depth of mixed layer as determined from temperature and salinity depth curves.

To summarize, it was shown that the change from neutral stability in the mixed surface layer to high stability in the pycnocline was abrupt and that the surface separating the two layers was one of dynamic significance. For this reason, the effective depth through which energy changes due to processes at the sea surface were distributed was assumed to be the mixed surface layer.

Further examination of figure 1 showed that the vertical density distribution is primarily a function of the vertical temperature distribution. The depth of the mixed layer could therefore be determined from temperature depth curves by using the first knee below the surface (excluding the diurnal thermocline) and Lumby's criterion that the isothermal layer be judged by the absence of temperature gradients in excess of 1° C. per 100 m.

B. DISTRIBUTION IN THE HAWAIIAN ISLANDS REGION

The definition of the mixed surface layer and an understanding of the vertical density and temperature relationships enable us to use bathythermograph observations in the Hawaiian region to determine the areal distribution of the depth of mixed layer. Thus, the pertinent data were taken from several thousand bathythermograms and assembled into monthly charts showing the distribution of the depth of the mixed layer (appendix B, chart I). The original data, their treatment, and manner of construction of the charts is described in appendix A.

Here, it should be mentioned that these charts have been based on data which were collected for diverse purposes at unrelated times. Information to be gained from them, therefore, is limited and attention will be focused on gross features in the distribution of the depth of mixed layer rather than details of individual contours. Even though many undulations in contours are believed to be due to shortcomings in the data, they have not been smoothed unless warranted by some evidence. One can say, however, although undulations in depth of the mixed layer contours may not reflect an actual situation, they do point to the fact that the ocean is not smooth and changes do not occur at regular time intervals. In that respect, then, they reflect reality.

A prominent feature in the January and February charts (chart I) is a trough in which the depth of the mixed layer is greater than in surrounding areas extending east to west between 15° and 20° N. Its depth is generally greater than 250 feet (76 m.), exceeding 400 feet (122 m.) west of 165° W. Another trough, centered about 165° W., extends from 30° N. southward and then eastward between the high islands and 25° N., where its depth is greater than 350 feet (107 m.). To the north of this feature is a shallow area, with a mixed layer depth of less than 200 feet (61 m.). The two troughs are separated by a ridge of less than 250 feet (76 m.) and a minimum depth of less than 150 feet (46 m.) in the northwest portion of the area.

South of the main east-west trough, between 10° and 15° N. and east of 175° W. (January), the depth of mixed layer is as shallow as 150 feet (46 m.) or less. In February, the shallow area is reduced in size by the deepening of the mixed layer west of 167° W. and along the southern boundary of the region. Also of interest here is the formation of a shallow "dome" at 15° N. and 163° W.

Charts for the months of March, April, and May, indicate a period of change. In March, although the January–February features are still evident, a change in the depth distribution of the mixed layer is beginning to take place. The small dome of February, at 15° N. and 163° W., has spread sufficiently to interrupt the main east-west trough between 158° and 163° W. In general, the depth of the mixed layer is decreasing throughout most of the survey area, except along the southern boundary, east of 162° W., where it is increasing. During April and May, the depth of the mixed layer continues to decrease throughout the survey area, except in the southern portion where it is increasing.

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[2] Personal communication, Mrs. Margaret Robinson, Scripps Institution of Oceanography.

In June, a new distribution pattern of the depth of the mixed layer has been established. A trough is now located between 10° N. and 13° N., west of 156° W., where the depth reaches approximately 300 feet (91 m.). East of 156° W. the trough, now 200 to 250 feet (61–76 m.) deep, turns northeastward. Over much of the area north of 20° N., the mixed layer is less than 100 feet (30 m.) deep.

The distribution of the depth of mixed layer during July and August does not differ materially from that during June. It shows little of interest north of 20° N., where the depth has increased but is still less than 150 feet (46 m.). The trough in the southern portion of the survey region remained between 10° and 15° N., except that it now curves northeastward between 160° and 165° W. with depths in excess of 300 feet (91 m.).

In the southeast portion of the region the depth has been steadily decreasing from about 200 feet (61 m.) in June to less than 100 feet (30 m.) in August.

The September depth of mixed layer chart shows that the trough has started, as it were, a northward movement and is now centered about 15° N., west of 160° W. with depths between 250 (76 m.) and 300 feet (91 m.).

In October, the trough has essentially resumed its winter (January and February) position. The depth north of 20° N. is increasing and the beginnings of the typical January and February structure are visible. This trend continues during November and December, and throughout this period the depth of mixed layer is shallow in the southern portion of the region.

The primary feature, then, of the distribution of the depth of the mixed layer in the Hawaiian region is a trough and seasonal differences in its location. Maximum development of this feature occurs in January, when the depth of the trough may exceed 400 feet (122 m.) and extends from east to west between 15° and 20° N. The June distribution typifies the other extreme, when it is found in its southernmost position. At this time the depth is also at a minimum in the northern portion of the region. It is interesting to note that the converse to the gradual northward motion of the mixed layer trough is not true during the March-April-May transition period. During that time the irregular depth distribution suggests disintegration of a pattern rather than a southward movement.

These features can also be illustrated by showing meridional profiles of the depth of mixed layer. The January and June profiles representing the mean depth of the mixed layer between 153° and 161° W. are given in figure 2A and those for 168° to 176° W. in figure 2B. The January profiles are similar. They show ridges in the vicinity of 12°, 20°, and 26° N. and troughs at 17°–18° N. and 23° N. The western profile is generally deeper than the eastern profile, except for the trough at 23° N. Both figures convey the impression of standing waves in the southern portion of the region, with nodes between 14° to 15° N. in the eastern portion and 12° to 13° N. in the western portion.

Although January and June exhibit extremes in the winter and summer distribution patterns, the depth of mixed layer during those months is not necessarily at the extreme in all portions of the survey region. To illustrate this, the maxi-

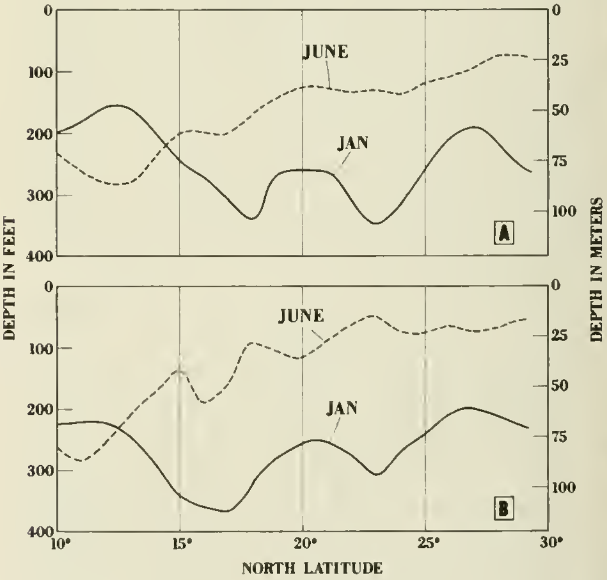


Figure 2.— Meridional profile of the depth of mixed layer in January and June, 10° to 30° N. Panel A, 153°–161° W.; panel B, 168°–176° W.

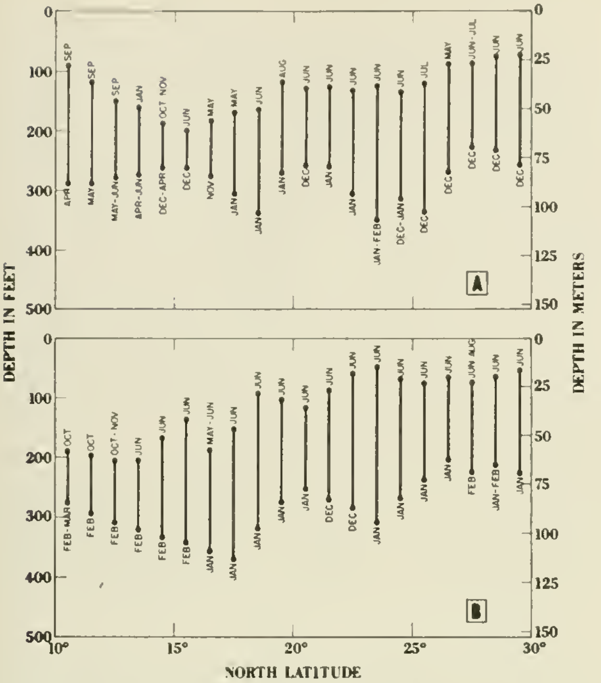


FIGURE 3.—Minimum and maximum mean depth of mixed layer 10° to 30° N. Panel A, 153°–161° W.; panel B, 168°–176° W.

mum and minimum depth of mixed layer has been indicated in figures 3A and B, together with the month of occurrence. These figures also indicate the annual depth range both in the eastern and western portion of the survey region between 10° and 30° N.

In figure 3A, for the eastern section, one notes that south of 14° N. the extremes in depth of the mixed layer occur in spring and autumn, whereas north of 15° N. they occur at the beginning of winter and summer. This suggests that the area south of about 14° N. belongs to a region with a different oceanographic climate, where extremes in the depth of the mixed layer follow those to the north of 14° N. by approximately three months.

Figure 3A also shows that the maximum difference in the average depth of the mixed layer between summer and winter is 220 feet (67 m.) and occurs at 23° N. The minimum difference occurs, as might be expected, at the nodal point, 15° N., where it is about 60 feet (18 m.). At 10° N. the seasonal range is again 200 feet (61 m.).

In the western section, figure 3B, the boundary between the two climatic regions lies at approximately 13° N. during the minimum depth of the mixed layer period. South of this latitude the minimum occurs in October (one month later than in the eastern section) and north of this latitude in June. During the maximum depth of the mixed layer period, the boundary is less distinct. At 10° N. the maximum occurs during February–March, between 11° and 15° N. in February, and north of 15° N. it occurs in January. This suggests that the boundary which separates the two climatic regions at 13° N. during the minimum depth of the mixed layer period, has shifted southward during the maximum depth of the mixed layer period. That is, in winter the western portion of the region between 10° and 30° N. lies within the same oceanographic climate.

Figure 3B also shows that the maximum difference in the average depth of the mixed layer between summer and winter is about 260 feet (79 m.) at 23° N., as in the eastern section. The minimum difference is about 90 feet (27 m.) at 10° N. Although a node is indicated between 12° and 13° N. in figure 2B, the minimum difference in the summer and winter depth of mixed layer did not occur at this latitude because of the apparent seasonal motion of the climatic boundary.

The mean seasonal variation in the depth of the mixed layer at 12°, 18°, 20°, and 22° N. in the meridinal storip between 153° and 161° W., is illustrated in figure 4. Comparison of the data for 12° N. with those to the north indicates the phase difference in extremes. It also shows that in the vicinity of the high islands of the Hawaiian archipelago the seasonal range in the depth of the mixed layer is less than that to either the north or south. Finally, figure 4 shows the seasonal variation in the depth of the mixed layer for the vicinity of 27° N. and 175° W. Here the depth decreases at a time (Dec. and Jan.) when it approaches the maximum throughout the northern portion of the region.

2. SURFACE TEMPERATURE

In oceanography as well as in weather analysis, temperature has long been recognized as an important climatic character. Surface temperature charts of the oceans, such as the U.S. Navy Hydrographic Office, Monthly Surface Temperature Charts of the North Pacific Ocean, (Misc. No. 10577), are readily available. A standard reference in oceanography is the temperature charts of Schott (1935). A new set of monthly temperature charts (appendix B, chart II) have been pre-

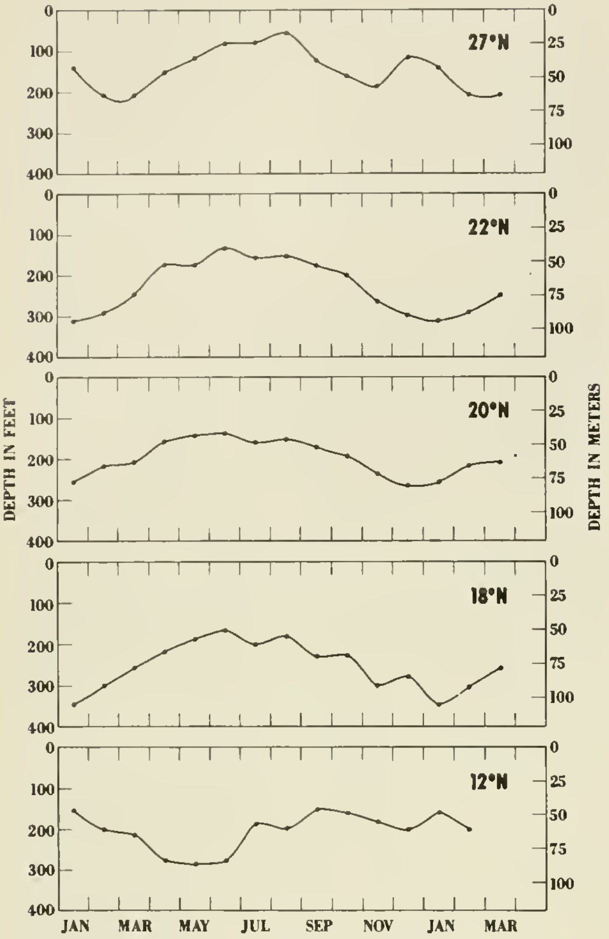


Figure 4.—Seasonal variation of the depth of the mixed layer at 12°, 18°, 20°, and 22° N., 153°–161° W., and at 27° N., 175° W.

pared for the Hawaii region, using the same bathythermograms mentioned in the previous section. Treatment of these data, and the manner of construction of the charts is discussed in appendix A.

The introductory comments of the previous section dealing with the distribution of the depth of the mixed surface layer also apply here. Attention will therefore again be focused on gross features in the distribution of the surface temperature rather than the details of individual contours. For example, if the irregular isotherm pattern to the southeast of the island chain in winter (chart II) were to be smoothed, the average temperature and its distribution would correspond well with the charts of Schott (1935) and those of the U.S. Hydrographic Office. It is believed, however, that these irregularities, persisting for several months, reflect large-scale mixing processes or eddies which may be real in nature.

Scanning the temperature charts one notes a parallel isotherm structure north of the island chain between November and April, with a latitudinal temperature gradient in the order of 1° to 1.5° F. (0.6° to 0.8° C.) per degree of latitude. In May, the beginnings of a change in the temperature structure become apparent, followed by the breakdown of the parallel isotherm pattern in June. The irregular temperature structure persists in the northern section of the region throughout July, August, and September, until, in October, isotherms become parallel again.

To the south of the island chain, the temperature structure is irregular during the winter and spring months. The temperature pattern from December through March, between 160° and 165° W., is suggestive of large-scale mixing processes or eddies.

The July, August, and September distributions show tongue-shaped areas of low temperature protruding westward in the southern portion of the region. Then, during October and November, it appears as if these tongues, between 155° and 165° W., were given a counterclockwise, 90° rotation, followed by disintegration into the irregular winter pattern.

The charts also show that minimum and maximum temperatures generally occur in March and September. In some areas, the minimum may occur in February and the maximum in either August or October. For these exceptions, however, the temperatures differ little from those in March and September. The March and September mean temperature profiles in figures 5A and B for the meridional strips between 153° to 161° W. and 168° to 176° W. therefore represent those for minimum and maximum temperature conditions.

During March, the temperature in the eastern section of the survey region (fig. 5A) decreases from about 78° F. (25.6° C.) at 10° N. to 75° F. (23.9° C.) at 17° N., at a rate of a little more than 0.4° F. (0.2° C.) per degree of latitude. After a slight increase of temperature just to the south of the Hawaiian Islands (also see chart II, March), the temperature decreases again northward to about 67° F. (19.4° C.) at 29° N., at an average rate of 1° F. (0.6° C.) per degree of latitude.

In the western section (fig. 5B), the March

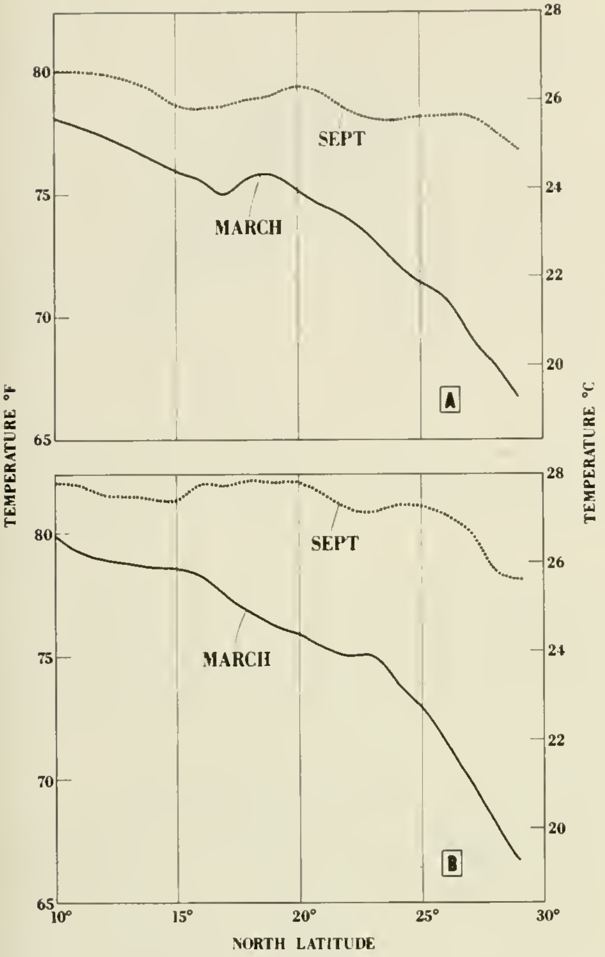


FIGURE 5.—Meridional profile of the surface temperature in March and September, 10° to 30° N.: panel A, 153°–161° W.; panel B, 168°–176° W.

surface temperature decreases in three distinct steps from 80° F. (26.7° C.) at 10° N. to 67°F. (19.4° C.) at 29° N.: First, between 10° and 16° N. at an average rate of 0.2° F. (0.1° C.) per degree of latitude; then between 16° and 23° N. at 0.5° F. (0.3° C.) per degree of latitude; and, finally, between 23° and 29° N. at 1.5° F. (0.8° C.) per degree of latitude.

During September, the temperature in the eastern section decreases from 80° F. (26.7° C.) at 10° N. to about 77° F. (25° C.) at 29° N. Equivalent temperatures in the western section are 82° F. (27.8° C.) and 78° F. (25.6° C.). Thus, there is an average decrease of 0.1° F. (0.06° C.) per degree of latitude in the eastern portion of the survey region and slightly more in the western section.

Although the changes in slope of the meridional temperature profiles cannot be explained at this time, they are believed to be of climatic significance. The temperature dips in September at about 15° N. in the eastern profile and about 13° N. in the western profile approximately correspond with the position of the depth of the mixed layer trough.

Finally, figures 5A and B show that the annual temperature range between 10° and 15° N. is approximately 2.5° F. (1.4° C.) both in the eastern and western section of the region. This increases to about 10.5° F. (5.8° C.) and 11.5° F. (6.4° C.) at 29° N. in the eastern and western sections, respectively, which is in good agreement with the charts of Schott (1935).

The mean zonal temperature profiles for 10° to 15° N., 15° to 20° N., 20° to 25° N. and 25° to 30° N, for March and September are shown in figure 6. For these months the temperature is approximately 3° F. (1.7° C.) higher in the western than in the eastern part of the region, except during September for the 15° to 20° N. and the 20° to 25° N. profiles, where the increases are 4° F. (2.2° C.) and 5° F. (2.8° C.), respectively.

Figure 6 also shows that the westward increase of temperature is not always gradual as it is between 25° and 30° N. during September, and between 20° and 25° N. during March. Between 15° and 20° N. it is stepwise both during March and September. Here, proceeding westward to about 157° W., the temperature decreases slightly and, then, during March, rises rapidly and remains fairly constant west of 160° W. During September, the temperature tends to continue the westward increase in a stepwise manner.

Between 10° and 15° N. the temperature again shows an initial westward decrease and, then, during March, an increase west of 160° W. During September, there is an increase west of 157° W., followed first by a leveling off and then another westward rise.

Between 20° and 25° N. the September westward temperature rise occurs mostly between 157° and 166° W. Thus, this temperature slope and those found in the eastern portion of the two profiles 10° to 15° N. and 15° to 20° N. may be of climatic significance, possibly delineating boundaries between climatic regions.

Finally, figure 7 has been included to show the seasonal temperature variation between 153°

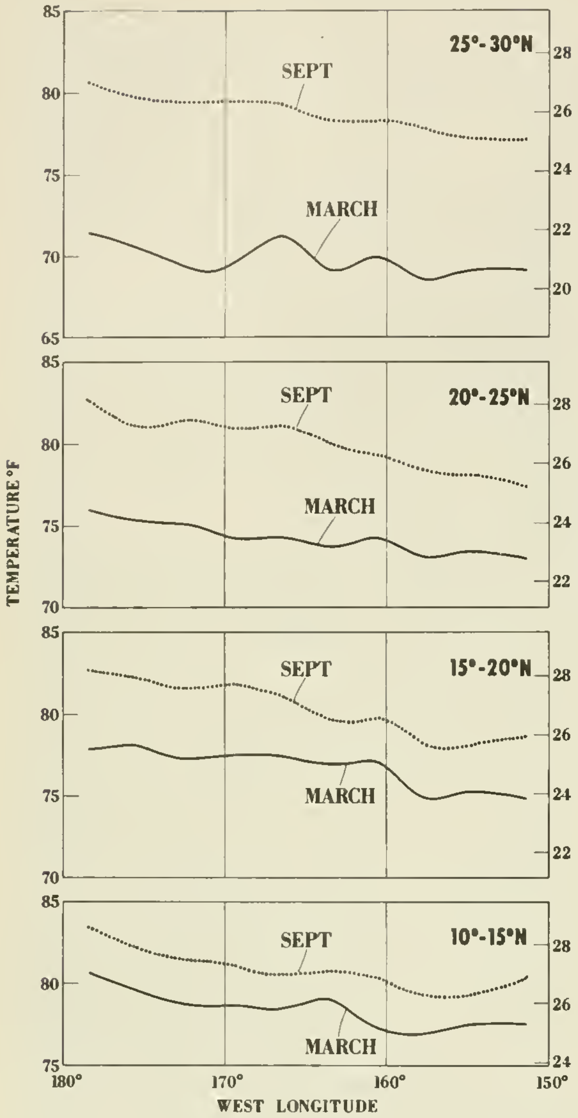


Figure 6.—Zonal profile of the surface temperature in March and September, 10°–15° N., 15°–20° N., 20°–25° N., 25°–30° N. and 150° W. to 180°.

and 161° W. at 12°, 17°, 20°, 22° and 26° N. It illustrates features which were demonstrated in previous figures. The seasonal temperature range increases only slightly northward from 3° F. (1.7° C.) at 12° N. to 5° F. (2.8° C.) at 22° N., and then almost doubles to 9.5° F. (5.3° C.) at 26° N. This is also reflected in the break of the meridional temperature gradient at 22° N. from November to May.

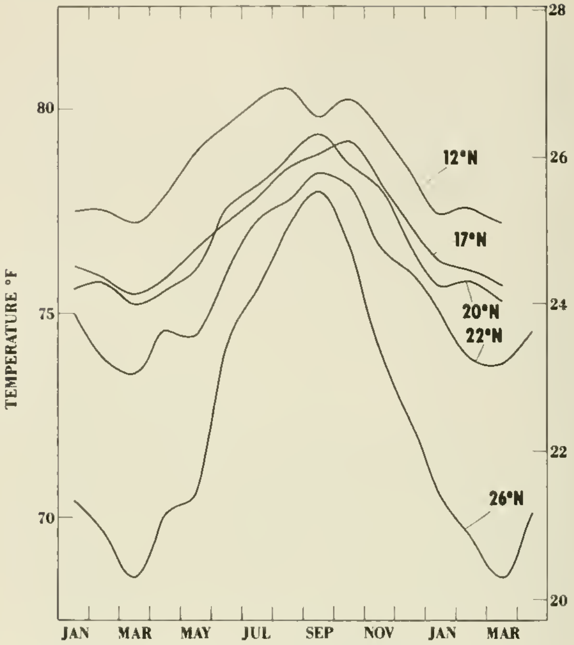


Figure 7.—Seasonal variation of the surface temperature at 12°, 17°, 20°, 22° and 26° N. between 153° and 161° W.

3. SURFACE SALINITY

The climatic indicator equivalent in importance to the temperature is the salinity. Unfortunately, in comparison with the temperature information, salinity data are scarce and it is therefore not possible to construct meaningful monthly charts. Despite this shortcoming, salinities obtained from oceanographic expeditions and from surface samples collected by Bureau of Commercial Fisheries vessels are sufficient to indicate features of climatic significance.

An attempt was made initially to locate the 35°/oo (salinity) isopleth throughout the year in the vicinity of the Hawaiian archipelago. This revealed that the isopleth started a generally northward movement in April, reaching an extreme position in July, as indicated in figure 8. It then begins a southward movement, reaching its extreme winter position (17° to 19° N.), during the November to February period. In the Hawaiian Islands the maximum salinity is therefore to be expected during November to February and the minimum during July.

There were also enough samples to show (fig. 9) the mean seasonal variation of salinity in the meridional strip between 155° and 160° W., at

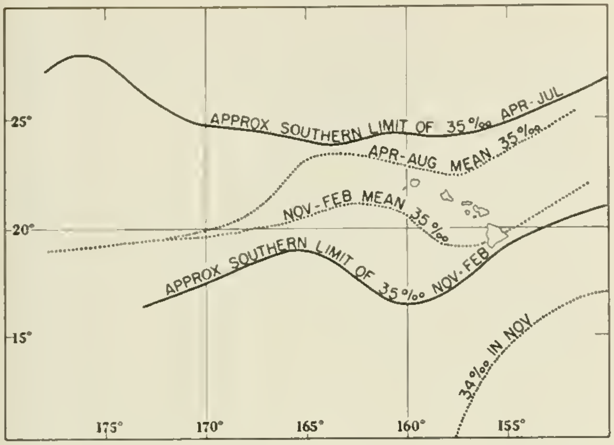


FIGURE 8.—Southern limit of the 35 °/oo salinity isopleth April to July and November to February, and mean location of the 35 °/oo salinity isopleth April to August and November to February.

13° N., 16° N., 21° N., 26° N., and the approximate salinity variation in the vicinity of Midway Island (28° N., 177° W.). Both at 16° N. and at 26° N. the minimum occurs during March and April, whereas at 21° N., within the island area, it occurs in July. The maximum salinity at 16° N. occurs during November and at 26° N. during November and December, whereas at 21° N. it occurs sometime during December, January, or February. The movement of the 35°/oo isopleth, therefore, coincides with the minimum and maximum salinity period at 21° N., but is out of phase with those to the north and south of the islands.

At 13° N. the salinity reaches a maximum in September and then in October begins to decrease rapidly, reaching a minimum in November. In the Midway Island region, beside the double maximum and minimum, the rapid decrease in salinity from a maximum between May and June to a minimum in July should be noted.

Finally, figure 9 shows that the seasonal salinity range is .50°/oo, .35°/oo, .25°/oo and .45°/oo at 13°, 16°, 21° and 26° N., respectively. At 21° N. it is therefore approximately 50 percent of that either at 13° N. or 26° N.

The salinity distribution between 155° and 160° W. can be illustrated further by meridional profiles. The lack of observations made it necessary to group the data for a number of months during the minimum and maximum salinity period at 21° N. Figure 10 shows the mean salinity profiles for April through August and for November through February.

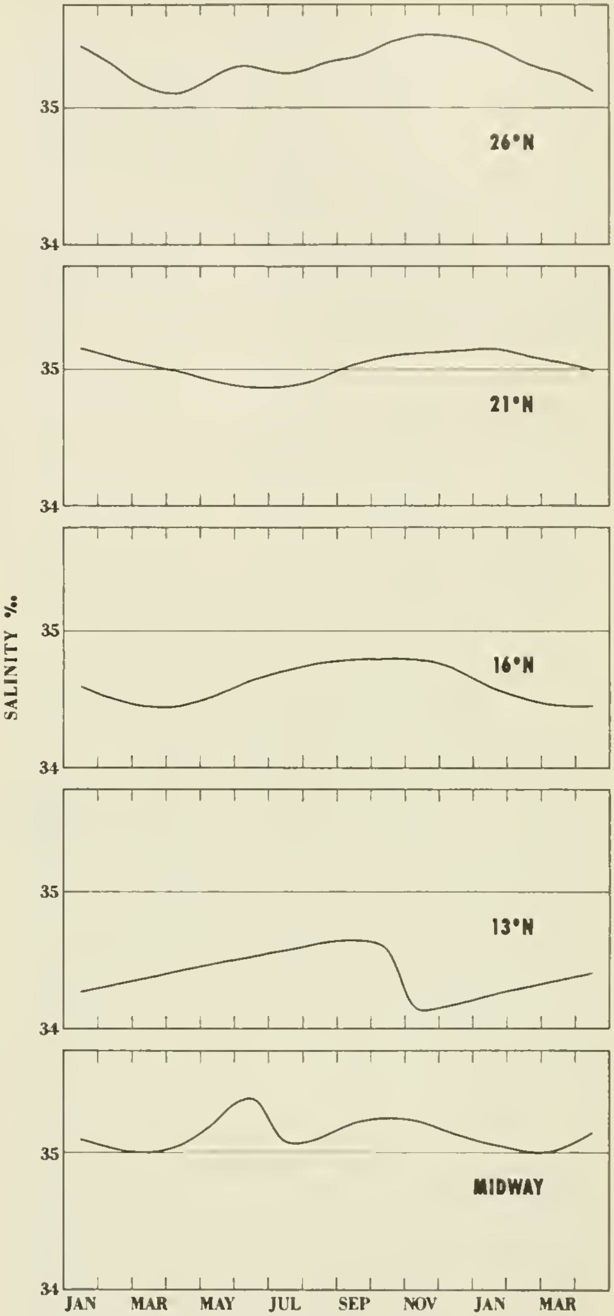


FIGURE 9.—Seasonal variation of the surface salinity at 13°, 16°, 21°, 26° N., between 155° to 160° W., and in the vicinity of Midway Island.

The low salinity profile (fig. 10A), representative of the June distribution, shows that the salinity increases northward from 34.65°/oo at 10° N. to 34.75°/oo at 20° N., or only by an average of .01°/oo per degree of latitude. The salinity then

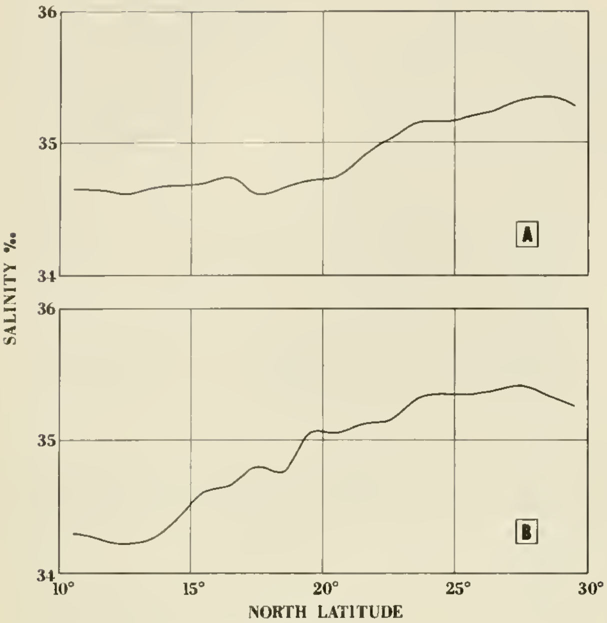


FIGURE 10.—Mean meridional salinity profile 10° to 30° N. between 155° and 160° W. Panel A, April to August; panel B, November to February.

rises at an average rate of .13°/₀₀ per degree of latitude to 35.15°/₀₀ at 23° N. It then increases to the maximum of 35.35°/₀₀ at about 28° N., at a rate of .04°/₀₀ per degree of latitude. Of importance here is the high salinity gradient within and slightly to the north of the Hawaiian Islands. This is indicative of a transition zone or boundary between different types of water. Data from individual months indicate that this boundary also moves seasonally with the previously described 35°/₀₀ isopleth, with which it is closely associated.

During the winter months or high salinity period in Hawaii (fig. 10B), the salinity decreases from 34.3°/₀₀ at 10° N. to a minimum of 34.2 °/₀₀ at 12° N. and then increases rapidly to 35.05°/₀₀ at 19° N., at an average rate of .12°/₀₀ per degree of latitude. North of 19° N. the salinity continues to increase to its maximum of 35.4°/₀₀ at about 27° N., at an average rate of .04°/₀₀ per degree of latitude. Of interest here is the southward shift of the high salinity gradient to south of 19° N. and the salinity decrease at 12° N. from 34.65 °/₀₀ during the April to August period to 34.2°/₀₀ during the November to February period.

Finally, two salinity charts were constructed (appendix B, chart III). Data were again grouped as above into the April to August and November to February periods. The charts will therefore reflect distributions for high and low salinity periods within the main islands area, but not for high and low periods for the remainder of the region.

Presenting data for groups of months reduces the differences in the distribution between months of extreme conditions. For example, figure 8 shows that the extreme positions of the 35°/₀₀ isopleth, corresponding to the months of July and January, are located farther apart than the equivalent isopleth on chart III. This is particularly so in the western portion of the region, where the mean April to August position of the 35°/₀₀ isopleth does not indicate its brief northward movement during July and August.

Despite this shortcoming, the charts provide information about the salinity distribution in the vicinity of Hawaii. During the April to August period the high salinity gradient between 20° and 25° N. is well defined in the eastern half of the region. Another high salinity gradient is indicated in the southeast corner of the region. Of particular interest is the appearance of two cells in which the salinity is higher than 35.4°/₀₀. A portion of one is located in the northeast corner and the other in the northern half of the region west of 172° W.

The salinity distribution for the November to February period when compared to the April to August distribution, suggests that the salinity gradient in the southeast corner of the region has moved northwestward and the gradient formerly in the Hawaiian Islands area has shifted southward. These then combined to form the more or less continuous salinity gradient illustrated in figure 10B.

In the northern portion there is now only one cell of high salinity (>35.4°/₀₀), which extends westward from about 157° W. This may mean that either the two high salinity cells of the April to August period have combined to form one, or that both have shifted eastward or westward, so that only one cell is apparent. Data collected by the Bureau of Commercial Fisheries during January to March, 1954 (McGary and Stroup, 1956: 55), suggest that the former is the case.

Reviewing the various fragments of information, one notes that to the north and south of the Hawaiian Islands low and high salinities occur approximately at the same time as low and high temperatures. In the vicinity of the islands, however, low and high salinities occur about three months later and at a time of minimum and maximum depth of the mixed layer. One also notes that the low salinities in the southeast portion of the region occur in the fall, approximately where the depth of the mixed layer distribution suggests a different oceanographic climate.

Finally, Midway Island is located in the vicinity of the salinity maximum, so that the sharp decline of about 0.35 °/₀₀ during July may be due to either a southward or a northward displacement of the high salinity cell. On the basis of chart III and figure 8 however, keeping in mind the scarcity of observations, the following postulate is favored: during the spring, the high salinity boundary moves northward east of 165°W. and northwestward west of this meridian, reaching Midway Island in July.

4. THE GEOPOTENTIAL TOPOGRAPHY

A fourth feature of importance in climatology is the geopotential topography, which is analogous to the pressure distribution in meteorology in that it provides a measure of the geostrophic currents. Again, data are inadequate to construct monthly charts. There have been no oceanographic expeditions to survey, as a primary objective, the region under investigation here. Dynamic height data have therefore been obtained chiefly from the Bureau of Commercial Fisheries Biological Laboratory (Honolulu) cruises in transit to other regions and from isolated expeditions passing through the area. Since potential gradients, rather than absolute values of dynamic height, are of importance in estimating geostrophic currents, combining isolated observations at different times of the year and from different years may result in charts materially different from the true flow pattern. Nevertheless, on the basis of availability and compatibility, data for the months of June through October and those for the months of December through April were combined into a summer and winter chart (appendix B, chart IV) to enable the reader to estimate the gross distribution of geopotentials.

The summer chart indicates that the subtropical convergence is approximately at 24° N., rather than at 31° N. as indicated by Schott (1935). It also shows that, as compared to the flow in the southeast portion of the region and that just south of the convergence between 158° and 170° W., there is a broad band of weak westerly flow to the southwest of the islands. Comparing the summer chart with the April to August salinity chart (chart III), one notes that the featureless geopotential distribution to the southwest of the islands corresponds with an equally featureless salinity distribution, both bounded by higher gradients to the northwest and southeast. It should be remembered that the combined data of the salinity chart are 2 months out-of-phase with those of the geopotential chart.

During the winter months, the subtropical convergence, as indicated in chart IV, (December to April) again lies to the south of the latitude indicated by Schott. In general, the area north of 20° N. appears to be one of very little net flow. In the southern portion of the region there is a large counterclockwise vortex centered at approximately 14° N. between 160° and 170° W. This feature was first apparent in data from *Hugh M. Smith* cruise 2, February 1950 (Cromwell, 1951, fig. 3) and occupies approximately the same area as the dome in the depth of the mixed layer during February (chart I).

Thus, although the geopotential topography as presented here should be regarded with caution, compatibility of special features, both with the salinity and the depth of mixed layer distributions, lends credibility to these charts.

PART II. PHYSICAL PROCESSES AND THEIR RELATION TO THE DISTRIBUTION OF SURFACE VARIABLES

In the first section of this atlas, patterns of distribution and regular periodic changes in the fields of temperature, salinity, depth of mixed surface layer, and geopotential were described. These features are associated to a varying degree of complexity with physical processes.

The importance of one or another process is usually not intuitively apparent. For example, the temperature of the water obviously depends on the heat exchange across the sea surface and the depth through which this is distributed, the manner in which heat is transported by currents, and other processes. It is not obvious, however, which one or combination of these factors determines the temperature of the water at any time or place. In order to gain an understanding of the physical processes, then, or to assess their relative importance, the problem must be formalized in accordance with principles discussed by Sverdrup et al. (1942). Here some of these principles will be applied to the distribution of the surface temperature, a variable of importance in any climatic study.

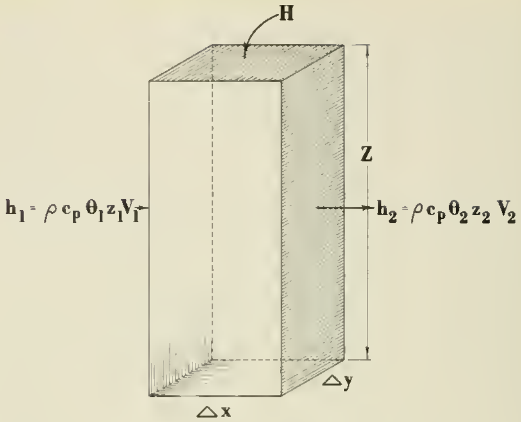
1. HEAT (SALT) BUDGET

On the basis of conservation of heat one can say that, at any locality in the ocean, the net heat exchange across the sea surface must be balanced by the change in heat content of the water column, heat diffused through the sides of the column, and the heat carried in or out of the column by means of currents. Such an expression can become complicated. However, since this is a climatic study, interest lies in the gross seasonal changes and, therefore, some simplifying assumptions can be made for the Hawaiian region (10°–30° N., 150° W.–180°).

In this area the mixed surface layer is generally well defined and since it has neutral stability one can say that heat exchange across the sea surface is uniformly distributed throughout this layer. Further, because of high stability in the thermocline just below the mixed layer, and small horizontal temperature gradients, vertical and lateral diffusion are assumed negligibly small compared to advection and heat exchange across the sea surface.

With these assumptions, a simple heat budget can be formulated in which the rate of change of heat content of a column of water of unit cross sectional area is balanced by the net heat exchange across the sea surface and the heat transported in and out by currents. This can be expressed in vector notation by

$$\frac{\partial(\rho c_p \theta z)}{\partial t} = H - \nabla\cdot(\rho c_p \theta z \overline{V}) \qquad (1)$$


H
Z
$h_1 = \rho c_p \theta_1 z_1 V_1$
$h_2 = \rho c_p \theta_2 z_2 V_2$
$\triangle y$
$\triangle x$

Here ρ is the density of the water and c_p its specific heat; θ is the temperature, z, the depth of the column of water (depth of mixed surface layer), and $\overline{V}$, the horizontal velocity. H is the net heat exchange across the sea surface and ∇, the two-dimensional operator

$$\bar{i}\frac{\partial}{\partial x} + \bar{j}\frac{\partial}{\partial y}$$

Similarly, the volume budget of the column of water is expressed by

$$\frac{\partial z}{\partial t} = -\nabla\cdot(z\overline{V}) \qquad (2)$$

Equations (1) and (2) can be expanded as follows, considering ρ and c_p constant:

$$z\frac{\partial \theta}{\partial t} + \theta\frac{\partial z}{\partial t} = \frac{1}{\rho c_p} H - \theta z \nabla\cdot\overline{V} - \theta\overline{V}\cdot\nabla z - z\overline{V}\cdot\nabla\theta \qquad (3)$$

$$\frac{\partial z}{\partial t} = -z\nabla\cdot\overline{V} - \overline{V}\cdot\nabla z \qquad (4)$$

After multiplying equation (4) by θ it can be subtracted from (3), leaving

$$z\frac{\partial \theta}{\partial t} = \frac{1}{\rho c_p} H - z\overline{V}\cdot\nabla\theta \qquad (5)$$

and then dividing by z, the temperature budget for a unit mass of surface water becomes:

$$\frac{\partial \theta}{\partial t} = \frac{1}{\rho c_p}\frac{H}{z} - \overline{V}\cdot\nabla\theta \qquad (6)$$

This equation is similar to equation V,5 in Sverdrup et al. (1942), except that the diffusion terms have been replaced by the heat exchange as a result of the simplifying assumptions.

Equation 6 can be divided into two portions: the term representing the temperature observations, and the terms representing the physical processes which determine the temperatures. Thus $\frac{\partial\theta}{\partial t}$, the local time change of temperature, represents the observed effect of those processes which appear on the right side of the equation.

The first one of these is associated with the net heat exchange across the sea surface, H. This is modified by the depth through which it is distributed, the density, and specific heat of the water, to appear as it affects the temperature of the water, in terms of temperature per unit mass per unit time, $\frac{1}{\rho c_p}\frac{H}{z}$.

The second term on the right side of equation 6 which affects the water temperature is the process of heat advection. It is an abstract term containing both the horizontal temperature distribution and the velocity and should not be mistaken for the heat transport. In expanded form the heat advection can be written $|V||\nabla\theta|\cos\phi$, i.e., the magnitude of the velocity (the speed) times the magnitude of the temperature gradient times the cosine of the angle between the direction of the current and the direction of the gradient. Thus, if ϕ is 90°, then the current flows parallel to the isotherms and the heat advection is zero, although the heat transport is not. Other cases where heat advection is zero occur when there are no currents or when there is no temperature gradient. The heat advection, therefore, is simply a process affecting the temperature of the water, here expressed in temperature per unit mass per unit time, resulting from a component of the current perpendicular to the isotherm. Even though the velocity enters into the expression, heat advection, if determined from budget considerations, can never give any information about the component of velocity parallel to the isotherm.

To summarize, the heat budget equation represents the manner in which the association between observed temperatures and physical processes has been formalized. It provides a qualitative appreciation of the processes involved and determines what parameters must be measured and the manner in which they should be measured. For example, it is necessary to obtain time series of observations together with horizontal distributions in order to be able to interpret temperature observations in terms of processes. Furthermore, if an understanding of the seasonal variation of processes is desired, then a plot of the local time change rather than the absolute temperature should be made.

The preceding discussion applies equally well to other parameters. For example, the salt budget equation is

$$\frac{\partial s}{\partial t}=\frac{s}{z}\,(E-P)-\overline{V}\cdot\nabla s \qquad (7)$$

where s is the salinity, and $E-P$ the evaporation minus precipitation. Here the processes are the water exchange across the sea surface and salt advection.

In the following sections the heat budget considerations will be applied to the Hawaiian region. First, the processes which transpire at the sea surface and affect the surface temperature will be described. These will then be combined with the data of part I to gain some understanding of the advection processes.

2. EVENTS AT THE SEA SURFACE

Events at the sea surface which affect the physical and dynamic properties of the surface water include the net heat exchange across the sea surface, evaporation minus precipitation, and the wind stress. In this part of the atlas, attention will be focused on those processes which affect the distribution of the surface temperature. Therefore, the net heat exchange across the sea surface will be of primary concern. The evaporation minus precipitation will be briefly discussed, omitting wind information which is commonly available in climatic compilations, such as the U.S. Navy Marine Climatic Atlas of the World, vol. II (1956), and others.

A. The Net Heat Exchange Across the Sea Surface

It has long been recognized that the ocean is a vast heat reservoir which has an important role in determining the climates of the world. Much work has been done to investigate the manyfold problems associated with the energy exchange at the air-sea boundary. A complete review of this research will not be attempted, but such general results as are of interest to this investigation may be found in Sverdrup et al. (1942) and Jacobs (1951).

Briefly, the processes of concern here are the radiant energy from sun and sky absorbed by the water (Q_s), the radiant energy lost due to back radiation (Q_b), heat energy lost by the processes of evaporation (Q_e), and conduction of sensible heat to or from the water (Q_c). The net heat exchange across a unit area of sea surface per unit of time, H, or the heat available to change the temperature of the water can be expressed by the formula:

$$Q_s - Q_b - Q_e - Q_c = H$$

These terms will now be discussed separately.

After entering the atmosphere, solar radiation is modified by scattering and absorption so that Q_o represents the energy reaching the earth's surface with a clear sky. Not all of this energy is absorbed by the water because of reflection, and further reduction may have occurred because of cloud cover. To compute the energy absorbed by the water (Q_s) the following expression has been given by Jacobs (1951):

$$Q_s = (1-r)(1-0.071\,C)Q_o$$

Here r is the percentage reflection and C is the cloudiness on a scale from 0 to 10. Q_s is generally expressed in cal. cm.$^{-2}$ day^{-1}.

Observations for the direct and diffuse solar radiation reaching the earth's surface, Q_o, are not available in the Hawaiian region, so that these values were obtained from the Smithsonian Meteorological Tables, table 135 (List, 1951), using a transmission coefficient $a=0.9$, and have been plotted in figure 11. At 10° N. the seasonal range of Q_o is 140 cal. cm.$^{-2}$ day^{-1}; from 640 cal. cm.$^{-2}$ day^{-1} in December to 780 cal. cm.$^{-2}$ day^{-1} in summer. At 30° N. the seasonal range is 460 cal. cm.$^{-2}$ day^{-1}; from 400 cal. cm.$^{-2}$ day^{-1} in December to 860 cal. cm.$^{-2}$ day^{-1} in June. It should also be noted that from April to September the difference between Q_o at 10° N. and at 30° N. is less than 100 cal. cm.$^{-2}$ day^{-1}, whereas in December this difference is 240 cal. cm.$^{-2}$ day^{-1}.

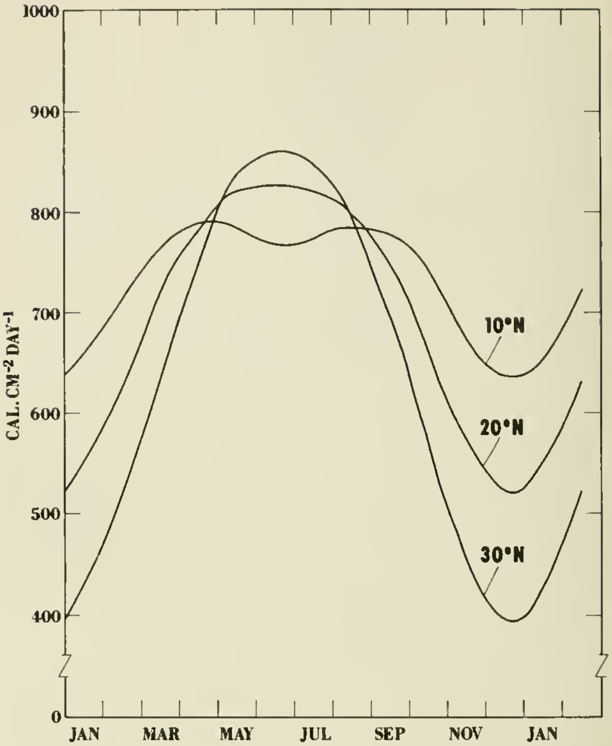


FIGURE 11.—Seasonal variation of the direct and diffuse solar radiation reaching the earth's surface at 10°, 20°, and 30° N.

On the basis of these data, even though the direct and diffuse radiation will be modified by factors, such as back radiation and evaporation, one would anticipate the following effects on the surface water temperature: (1) the seasonal temperature range increases northward, and (2) the water temperature difference between 10° N. and 30° N. would be greatest during the minimum temperature period of the year.

In order to use Jacobs' formula, the cloud cover, which ranges from four- to six-tenths of sky covered in the Hawaii region, was obtained from the U.S. Weather Bureau Atlas of climatic charts of the ocean (McDonald, 1938). The amount of radiation reflected back to the sky was quoted by Jacobs (1951) to range from 3.3 percent at the equator to 8 percent at the poles. With these data and Q_o from the Smithsonian tables, the amount of radiation absorbed in the water, Q_s, was computed.

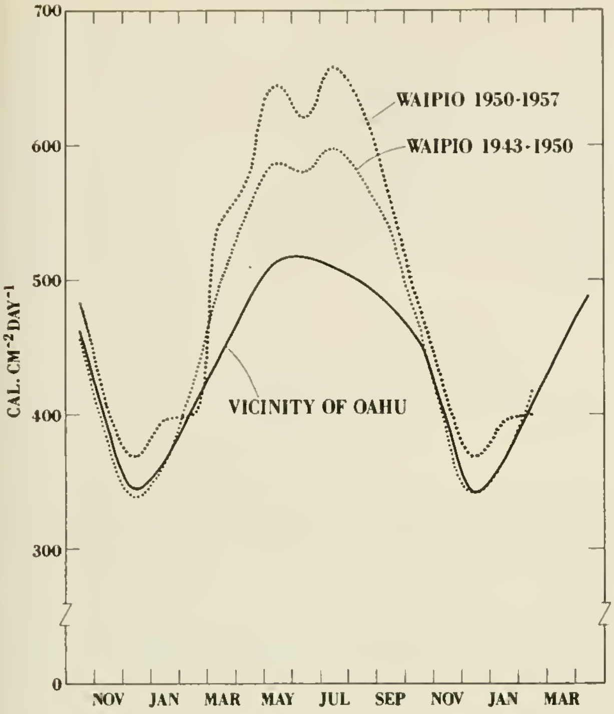


FIGURE 12.—Amount of computed radiation absorbed by the water (Q_s) in the vicinity of Oahu, and measured radiation reaching the surface at Waipio, Oahu, mean 1943–50, and mean 1950–57.

Figure 12 shows the results of this computation for the vicinity of the island of Oahu. The heat absorbed by the water ranges from 340 cal. cm.$^{-2}$ day^{-1} in December to 510 cal. cm.$^{-2}$ day^{-1} in June. Comparable values for a clear sky at 20° N. (fig. 11) are 520 cal. cm.$^{-2}$ day^{-1} and 830 cal. cm.$^{-2}$ day^{-1}, respectively. In the vicinity of the Hawaiian Islands, cloud cover, therefore, reduces the insolation by about 35 to 40 percent.

Although no direct measurements of Q_s for the marine vicinity of Oahu are available, the radiation reaching the surface has been measured at Waipio (near Pearl Harbor), Oahu, by the Sugar Planters Association and the Pineapple Research Institute of Hawaii. The mean data for the years 1943 to 1950 and 1950 to 1957 have been plotted in figure 12.[3]. The mean observed solar radiation from November through February for the 1943–50 period is approximately the same as that computed for the vicinity of Oahu. During the remainder of the year, the computed values are up to 80 cal. cm.$^{-2}$ day^{-1} (about 15 percent) too low. The mean observed values for the 1950–57 period are about 30 cal. cm.$^{-2}$ day^{-1} higher in winter and up to 140 cal. cm.$^{-2}$ day^{-1} (about 25 percent) higher in summer than the computed values. In other words, the computed insolation values are of the right order of magnitude, in good agreement with observed values during the winter, but 15 to 25 percent too low during the summer.

The seasonal discrepancy between the computed and observed insolation can be explained in several ways. During the winter months medium and high clouds are an important part of the cloud cover, whereas during the remainder of the year trade wind cumuli predominate. First, then, the discrepancy may be due to seasonal variations in the difference between the cloudiness over Waipio, located on the leeward side of the island, and that over the ocean, since orography would affect low, tradewind cloudiness more than medium and high cloudiness. In addition the cloud correction formula may be sufficiently accurate for the medium and high cloudiness during the winter, but not for the trade wind cumuli in summer. Since cloud cover is observed obliquely from a ship, there is a tendency to overestimate cover of the latter type. Furthermore, the formula used above does not take into consideration the reflection from trade wind cumuli.

The next term to be considered in the net heat exchange across the sea surface is the back radiation. This is a function of the absolute surface temperature of the sea, radiating almost like a black body, the relative humidity, and the type and amount of the cloud cover. According to Sverdrup et al. (1942:112) back radiation can then be expressed by

$$Q_b = Q_{bo} (1 - 0.083C).$$

This applies to average conditions only, since the reduction of the effective back radiation, Q_{bo}, due to clouds depends upon the altitude and the density of the clouds. C is the cloudiness on the scale from 0 to 10.

The necessary data to compute the back radiation were obtained from the Atlas of Climatic Charts of the Ocean (McDonald, 1938) and from Sverdrup et al. (1942: fig. 25). Back radiation in the Hawaiian region ranged from 115 to 150 cal. cm.$^{-2}$ day^{-1}, and in the vicinity of Oahu from 130 to 150 cal. cm.$^{-2}$ day^{-1}, with the lower values occurring during spring and summer.

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[3] Data were supplied by Dr. Paul C. Ekern, Pineapple Research Institute, Honolulu, Hawaii.

Again, no observations of back radiation are available and, as before, the principal error would be due to an incorrect cloud factor for the trade wind area.

Next in the net heat exchange across the sea surface is the evaporation. Its importance to the net heat exchange can be gauged from the fact that about 585 calories are used to evaporate 1 gram of sea water. No observations for Q_e are available, so that computed values must be used. These are based on formulae described both by Sverdrup and others (1942) and Jacobs (1951). They suggested simplified formulae for use with average climatic data to obtain the evaporation as a function of the sea and air vapor pressure difference and the wind speed. Albrecht (1951) computed the evaporation for the Indo-Pacific using the formula from Sverdrup (1936) and the meteorological data of the revised, 1944, German edition of McDonald (1938). In checking his results by means of the total Indo-Pacific water budget, he estimated the calculated evaporation to be 10 percent too low. Since most meteorological observations at sea are made from merchant ships, Albrecht assumed height-of-bridge (8 m.) for psychrometric observations and masthead (20 m.) for wind observations. By assuming both observations to be made at bridge height (8 m.), the computed evaporation would be 10 percent higher.

For computations of the net heat exchange in this paper, revised evaporation charts, received from Dr. Albrecht in a personal communication, were used. Figure 13 shows the seasonal variation in the heat used for evaporation at 20° N. and 160° W. It peaks at about 330 cal. cm.$^{-2}$ day^{-1} in April, with the low evaporation period extending from July to January at 220 to 250 cal. cm.$^{-2}$ day^{-1}.

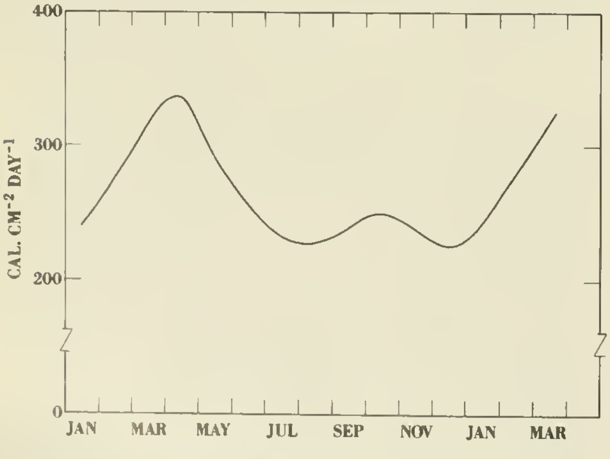


Figure 13.—Seasonal variation in the heat used for evaporation at 20° N. and 160° W.

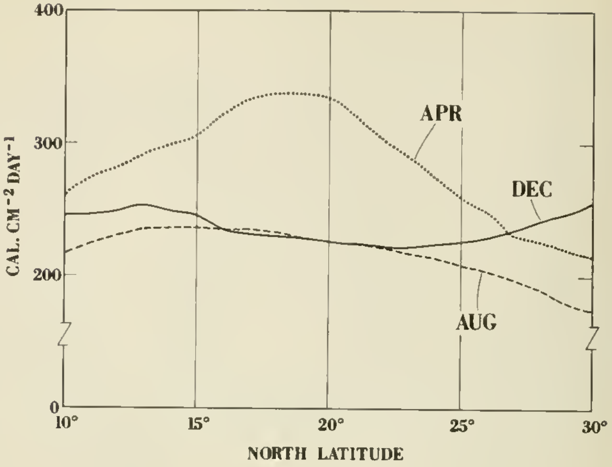


Figure 14.—Meridional profiles of the heat used for evaporation, 160° W. during April, August, and December.

Meridional profiles of the heat used for evaporation at 160° W. are shown in figure 14. In April, during the maximum evaporation period at 20° N., it is 260 cal. cm.$^{-2}$ day^{-1} at 10° N., 340 cal. cm.$^{-2}$ day^{-1} at 18° N., and 210 cal. cm.$^{-2}$ day^{-1} at 30° N. In August, during the minimum evaporation period at 20° N., it is 220 cal. cm.$^{-2}$ day^{-1} at 10° N., 240 cal. cm.$^{-2}$ day^{-1} at 17° N., and 170 cal. cm.$^{-2}$ day^{-1} at 30° N. In December, the evaporation is 240 cal. cm.$^{-2}$ day^{-1} at 10° N., 220 cal. cm.$^{-2}$ day^{-1} at 22° N., and 260 cal. cm.$^{-2}$ day^{-1} at 30° N.

It should be noted that whereas maximum and minimum periods of evaporation at 20° N. occur in April and August, at 30° N. they occur in winter and summer (December and June), respectively, illustrative of different climatic areas.

Riehl and others (1951) obtained an almost exact heat balance in the atmosphere northeast of Hawaii by using heat equivalents for evaporation based on Jacobs' method of computation. The values based on weather-ship observations during July to October 1945 yielded evaporations of 230 to 250 cal. cm.$^{-2}$ day^{-1} for 26° N., 149° W. and Oahu, respectively. These are in good agreement with Albrecht's results. Although Riehl's values were obtained by essentially the same method as Albrecht's, they do provide an indirect check in that they also balanced the heat budget of the atmosphere.

The last term to be considered in the net heat exchange across the sea surface is conduction of sensible heat. It is a function of the vertical temperature gradient and turbulence above the sea surface. From Jacobs (1951), one again obtains a simple expression when average climatic data are considered:

$$Q_c = 1.45(\theta_w - \theta_a)\, W_a \text{ cal. cm.}^{-2} \text{ day}^{-1}.$$

θ_w and θ_a are the temperatures in °F. of the sea and air, respectively, and W_a is the wind speed in knots.

In the Hawaiian region, the exchange of sensible heat across the sea surface is not important and ranges from 5 to 40 cal. cm.$^{-2}$ day^{-1}, with the high values occurring during winter months in the northern portion of the region. In the vicinity of the main island group, it ranges from 4 cal. cm.$^{-2}$ day^{-1} in August to 25 cal. cm.$^{-2}$ day^{-1} in February.

To summarize, figure 15 shows the relative magnitude of the terms discussed in this section, as they affect the net heat exchange at 20° N., 100° W. It is apparent that the heat absorbed by the water, Q_s, determines the seasonal pattern of the net heat exchange, H, although this may be modified, as it is during the months centered about April, because of high evaporation rates.

The total rate of heat loss from the sea surface is at a maximum of 490 cal. cm.$^{-2}$ day^{-1} during April and at a minimum of 370 cal. cm.$^{-2}$ day^{-1} during July and August. During the former period, the relative contribution to the total daily heat loss from back radiation, evaporation and conduction is 27 percent, 69 percent, and 4 percent, respectively. During the latter period, these relative losses are 37 percent, 62 percent, and 1 percent, respectively. This illustrates again the importance of evaporation in the net heat exchange across the sea surface.

The relative importance of the terms contributing to the net heat exchange across the sea surface is also illustrated in figure 16 by meridional profiles at 160° W. for June and December. During June (fig. 16A), the rapidly rising net heat exchange north of 19° N. is seen to be due to northward declining evaporation from 260 cal. cm.$^{-2}$ day^{-1} at 19° N. to 130 cal. cm.$^{-2}$ day^{-1} 30° N. In December (fig. 16B), the total daily heat loss across the sea surface varies only by about 30 cal. cm.$^{-2}$ day^{-1} between 10° and 30° N.

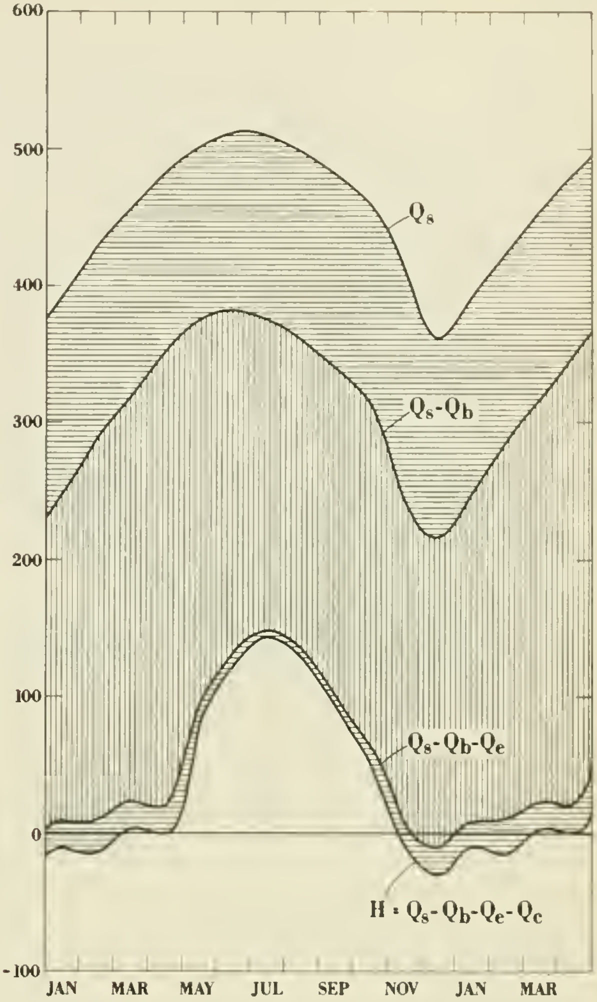


FIGURE 15.—Relative magnitude of the components entering into the net heat exchange across the sea surface at 20° N., 160° W. (Q_s—heat absorbed by the water, Q_b—back radiation, Q_e—heat used for evaporation, Q_c—conduction of sensible heat, H—net heat exchange across the sea surface.)

It is now of interest to know how the net heat exchange affects the surface temperature of the water. According to the basic assumptions of the previous section, the absorbed heat remaining in the water after back radiation, evaporation, and conduction, would be uniformly distributed throughout the mixed layer. Therefore, according to equation 6, one obtains the change of surface temperature per month by dividing the net heat exchange, H, by the depth of mixed

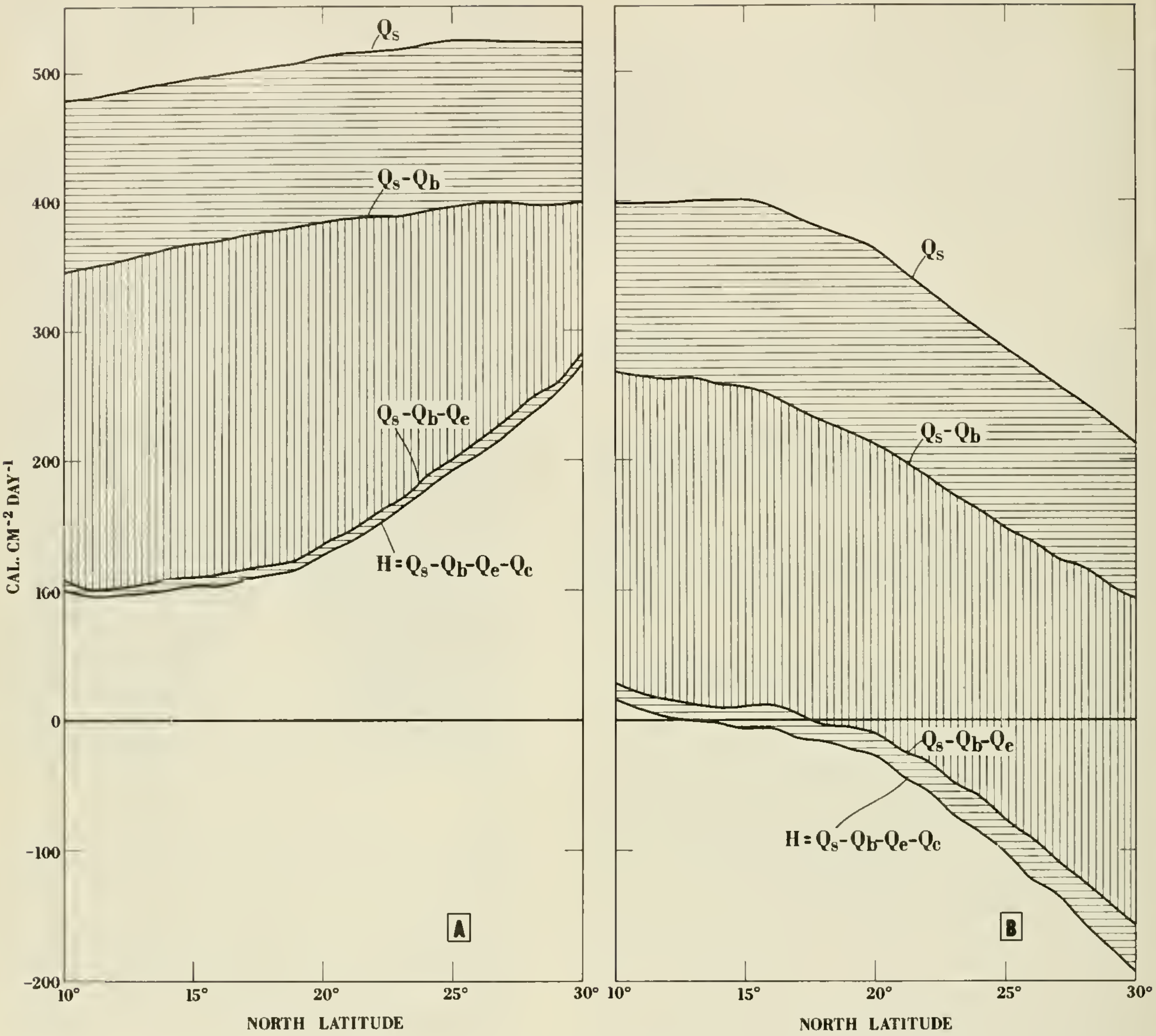


FIGURE 16.—Meridional profiles showing the relative magnitude of the components entering into the net heat exchange across the sea surface at 160° W. Panel A—June, panel B—December. (Q_s—heat absorbed by the water, Q_b—back radiation, Q_e—heat used for evaporation, Q_c—conduction of sensible heat, H—net heat exchange across the sea surface.)

layer, z, the specific heat, c_p, and the density of sea water, ρ.

This is illustrated in figure 17 by the meridional profile of the net heat exchange and the equivalent change of temperature at 160° W. in June and December. For convenience the net heat exchange is presented in units of kilocalories per square centimeter per month (kcal. cm.$^{-2}$ mos.$^{-1}$). At 12° N., for example, the net heat exchange varies from approximately +0.3 kcal. cm.$^{-2}$ mos.$^{-1}$ in December to +3.0 kcal. cm.$^{-2}$ mos.$^{-1}$ in June; a tenfold increase. The effect on the change of surface temperature, on the other hand, varies from about 0.1 °C. mos.$^{-1}$ to 0.3 °C. mos.$^{-1}$, only a threefold increase, reflecting the effect of the seasonal change in the depth of mixed layer at 12° N. (fig. 2).

At 30° N. the net heat exchange varies from about +7.9 in June to −5.9 kcal. cm.$^{-2}$ mos.$^{-1}$ in December. The equivalent change of surface

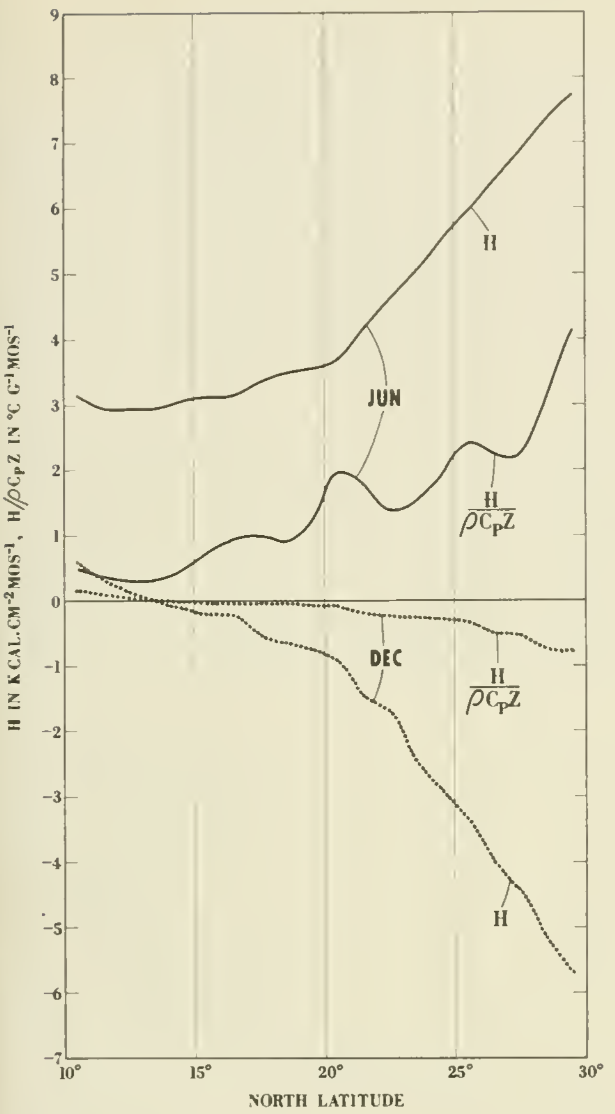


Figure 17.—Meridional profile at 160° W. of the net heat exchange and its equivalent rate of change of surface temperature during June and December.

temperature during those months would vary from about +4.5 °C. mos.$^{-1}$ to -1.0 °C. mos.$^{-1}$, respectively, again reflecting the effect of the seasonal change in the depth of mixed layer.

In the surface temperature discussion reference was made to the northward increase in the seasonal temperature range (figs. 5 and 7). For example, at 12° N. it is only 1.7 °C., whereas at 26° N. it is 5.3° C. Figure 17 shows that the seasonal range in the rate of change of temperature attributable to the net heat exchange to be only 0.2° C. mos.$^{-1}$ at 12° N., but 2.7° C. at 26° N. On the basis of the seasonal range of the net heat exchange, one would therefore expect a northward increasing, seasonal temperature range.

In the discussion of figure 7 reference was also made to the break in the meridional temperature gradient at 22° N. during November to May. This was attributed to a boundary of climatic significance. Such a boundary would be one south of which the net heat exchange is positive throughout the year and north of which it is positive during the summer and negative during the winter. Figure 17 shows this to occur at about 13° N. rather than at 22° N. as anticipated from figure 7. Further examination of figure 17, however, shows that the effect ol the depth of the mixed layer is such that the monthly temperature change due to net heat exchange, although negative, remains negligibly small (0.1°C. mos.$^{-1}$) to 20° N. Therefore, again on the basis of net heat exchange as expressed in temperature change per month, one would expect the meridional temperature gradient to increase north of 20° N.

To show the mean meridional profile, between 150° W. and 180°, of the net heat exchange and its effect on the change of surface temperature, figure 18 has been included. It is similar to figure 17, except that it shows the net heat exchange to be positive throughout the year south of 18° N. Thus, certain features in the distribution of surface temperature appear to be associated with the net heat exchange across the sea surface.

Finally, the climatic boundary referred to above (where the negative change of temperature due to heat exchange becomes greater than 0.1° C. per month) may be of dynamic and biological significance. In those latitudes where the net heat exchange is always positive, it has a stabilizing influence on the water column throughout the year. To the north of the boundary, where the effect on the temperature decline is no longer negligible, the net heat exchange has a stabilizing effect tending to oppose the effect of wind stirring, during part of the year, and during the remainder of the year, when it is negative, tends to aid the effects of wind stirring by convection.

Biologically this boundary may be regarded as one which separates high and low latitude indices of production. For example, on the low latitude side nutrients in the water and plankton standing

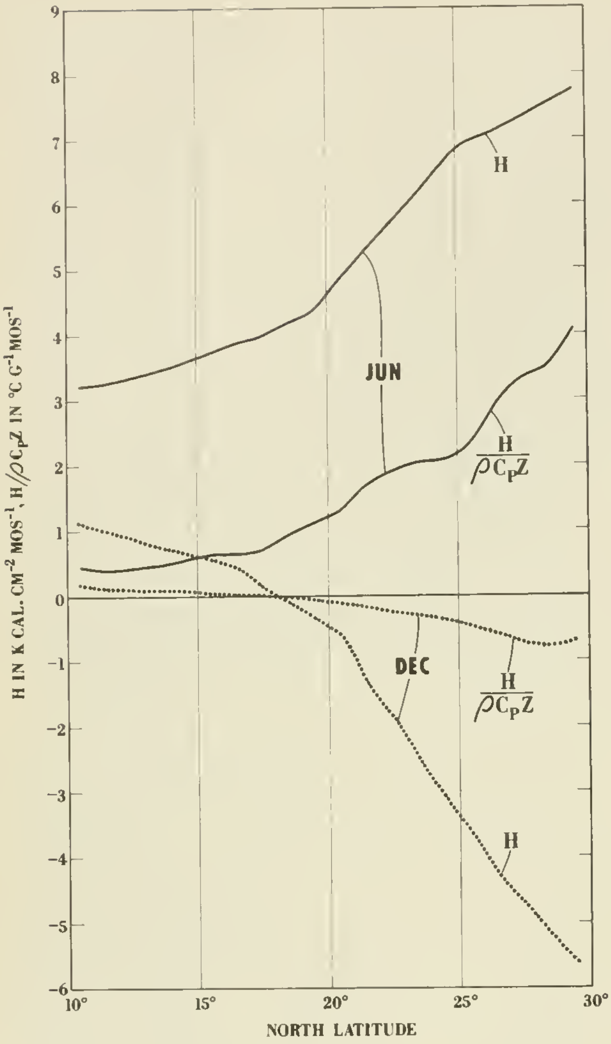


Figure 18.—Mean meridional profile (150° W.–180°) for the Hawaiian survey region of the net heat exchange and its equivalent change of surface temperature during June and December.

crops would show small seasonal variations, whereas on the other side these seasonal variations would increase toward higher latitudes.

B. Evaporation Minus Precipitation

The term in the salt budget (equation 7) which would be equivalent to the heat exchange in the heat budget (equation 6) is the freshwater exchange across the sea surface or the evaporation minus precipitation ($E-P$). Evaporation has the effect of increasing the surface salinity and precipitation of decreasing it. Although the salinity data in part I are inadequate for salt budget computations, they are sufficient to warrant a brief discussion of the evaporation minus precipitation.

Albrecht (1951), in connection with the water budget of the Indo-Pacific, computed the precipitation. His work was based on a revision of Schott's (1935) mean annual precipitation charts, McDonald's (1938) charts of frequency of precipitation, and precipitation data from island and coastal stations. Figure 19 shows the seasonal, meridional distribution of evaporation minus precipitation at 160° W., based on the revised charts of Albrecht (1951), received in a personal communication.

The northward progression of the maximum ($E-P$) with time is apparent. At 15° N. it occurs during December, at 20° N. in April and May, and at 28° N. during October. Maximum ($E-P$) is centered about 20° N. and the months about July, when it is higher than 10 cm. per month. Maximum and minimum ($E-P$) at 10° to 15° N. coincides with minimum and maximum

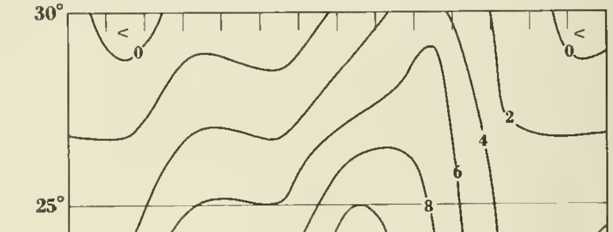


Figure 19.—Seasonal evaporation minus precipitation along 160° W. in cm. mos.$^{-1}$.

$(E-P)$ at 25°–30° N., respectively. An excess of precipitation over evaporation occurs south of 15° N. between March and December, reaching farthest north during September and October. Excess precipitation over evaporation also occurs north of 29° N. in February.

The seasonal variation of $(E-P)$, together with the variation of evaporation as plotted in figure 20 for 20° N. 160° W., illustrates the manner in which precipitation modifies the evaporation. The precipitation is approximately 1.2 cm. mos.^{-1} in July and 7.2 cm. mos.^{-1} in December and January.

Meridional profiles of $(E-P)$ and evaporation at 160° W., illustrating the modifying effect of precipitation, are shown in figure 21. In April, at the time of maximum evaporation at 20° N., the minimum precipitation of 4.8 cm. mos.^{-1} occurs at 22° and 23° N. It increases northward to 10 cm. mos.^{-1} at 30° N. and southward to 16 cm. mos.^{-1} at 10° N. In August precipitation is essentially lacking between 21° and 24° N., but it increases northward and southward to 6 cm. mos.^{-1} at 30° N. and 16.4 cm. mos.^{-1} at 10° N. Finally, in December, the time of maximum $(E-P)$ at 15° N., minimum precipitation of 7 cm. mos.^{-1} has shifted southward along the meridian to 16° N., with 12.4 cm. mos.^{-1} and 10.6 cm. mos.^{-1} at 30° and 10° N., respectively.

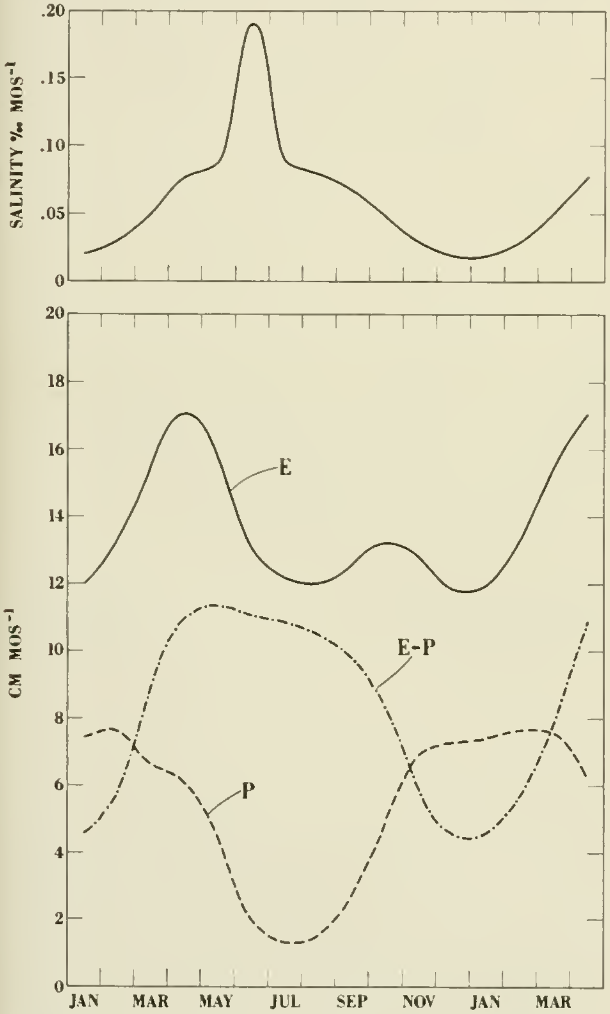


FIGURE 20.—Seasonal variation at 20° N., 160° W., in the rate of evaporation, precipitation, evaporation minus precipitation and equivalent salinity change per month (upper panel).

In order to illustrate the effect of evaporation minus precipitation upon the salinity in terms of change of salinity per month, equation 7 states that $(E-P)$ must be divided by the depth of the mixed layer and multiplied by the salinity. The upper panel in figures 20 and 21 shows the change of salinity due to $(E-P)$ in terms of parts per thousand of salt per month. Thus, at 20° N. 160° W., figure 20, the evaporation minus precipitation would increase the salinity by 0.02‰ mos.^{-1} in December and January, 0.09‰ mos.^{-1} in May and July, and in June by 0.19‰ mos.^{-1} because of the shallow depth of mixed layer.

In figure 21 the April maximum change of salinity of 0.09‰ mos.^{-1} occurs at 23° N. (maximum $(E-P)$ occurs at 20° N.). During August the maximum change of 0.1‰ mos.^{-1} occurs at 22° N., and in December the maximum of 0.04‰ mos.^{-1} occurs at 13° N. During December the change of salinity due to evaporation minus precipitation is positive along the entire section shown, whereas during April and August it is negative south of 13° and 15° N., respectively.

The seasonal changes of salinity at 13°, 16°, 21°, and 26° N. (fig. 9) can now be examined in the light of the evaporation minus precipitation. At each of these latitudes except 13° N., $(E-P)$ is positive throughout the year, so that declining salinities cannot be explained by excess precipitation, but must be associated with movement of the surface water.

At 21° N. the salinity is declining and reaches a minimum when the monthly change of salinity due to $(E-P)$ is rising and reaches a maximum. This phenomenon can be explained by the northward movement of the high salinity gradient or boundary described on page 382 (fig. 10).

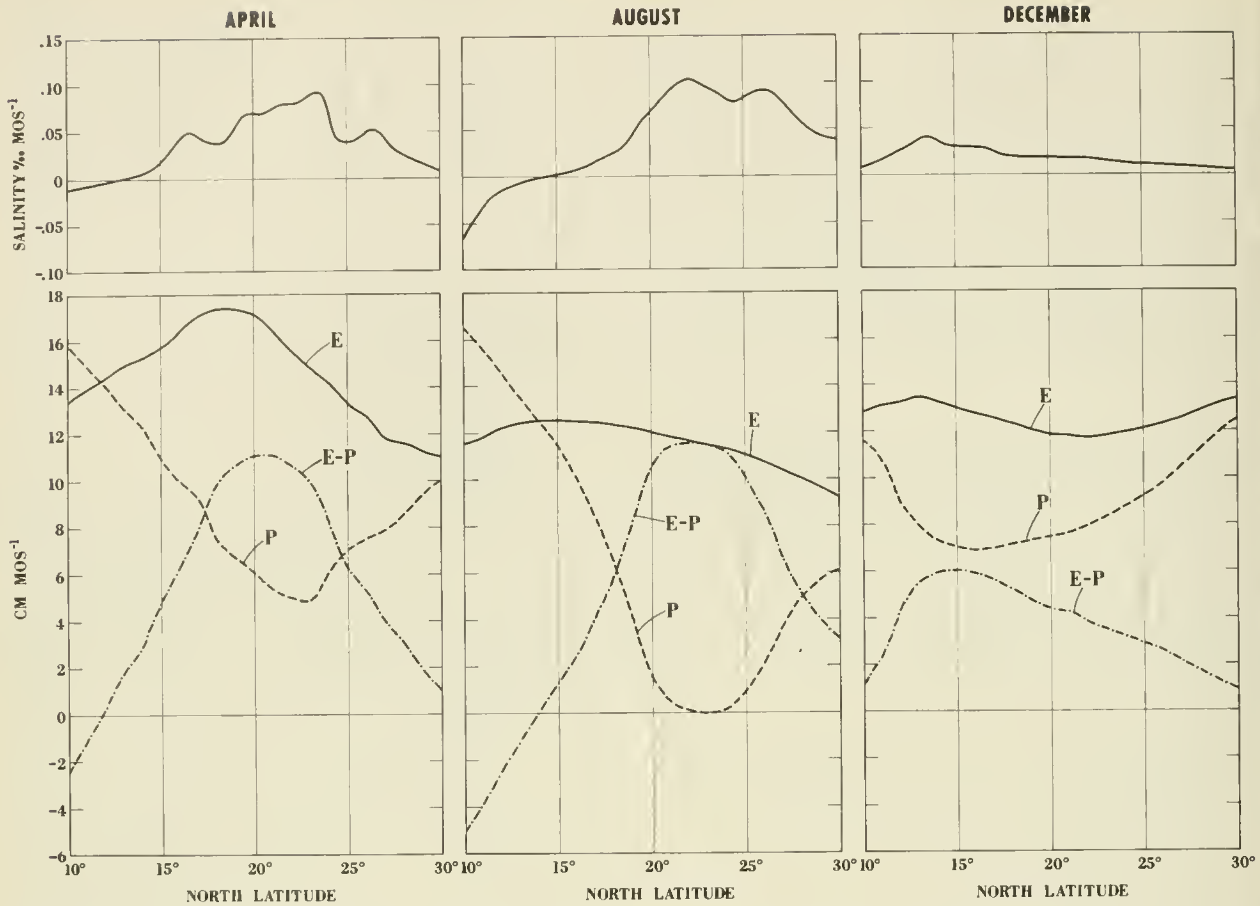


Figure 21.—Meridional profiles at 160° W. of evaporation, precipitation, evaporation minus precipitation, and equivalent salinity changes per month (upper panel) during April, August, and December.

It is also difficult to explain the sudden drop of salinity at 13° N. during October and November (fig. 9) in terms of evaporation minus precipitation. Here the decline of salinity occurs at the very time when there is a change from excess precipitation to excess evaporation. As at 21° N., this indicates the movement of a boundary, possibly due to the same forces which are involved in the rapid change of $(E-P)$.

3. ADVECTION

A. Characteristic Advection Diagram

The simplified heat (temperature) budget equation (equation 6) contains only three terms. Therefore, by using the temperature data from part I and the net heat exchange across the sea surface from the previous section, one can obtain a measure of the advection. This is best accomplished by drawing $\frac{H}{\rho c_p z}$ and $\frac{\Delta\theta}{\Delta t}$ versus time for any one location. Then, as the approximate temperature budget $\frac{H}{\rho c_p z}-\frac{\Delta\theta}{\Delta t}=\overline{V}\cdot\nabla\theta$ shows, the difference between the two curves indicates the magnitude of advection.

Figure 22 shows the $\frac{H}{\rho c_p z}$ and $\frac{\Delta\theta}{\Delta t}$ curves for the three-degree squares 14° to 17° N., 156° to 159° W., 20° to 23° N., 156° to 159° W., and 26° to 29° N., 156° to 159° W. One notes that the shape of the curves changes with location. For example, to the south of the islands the heat exchange across the sea surface, as it affects the surface temperature, reaches its maximum during September and October and its minimum during January. In the vicinity of the islands, the maximum occurs during July and the minimum during December. Finally, to the north of the islands the maximum heat exchange occurs in June and the minimum occurs

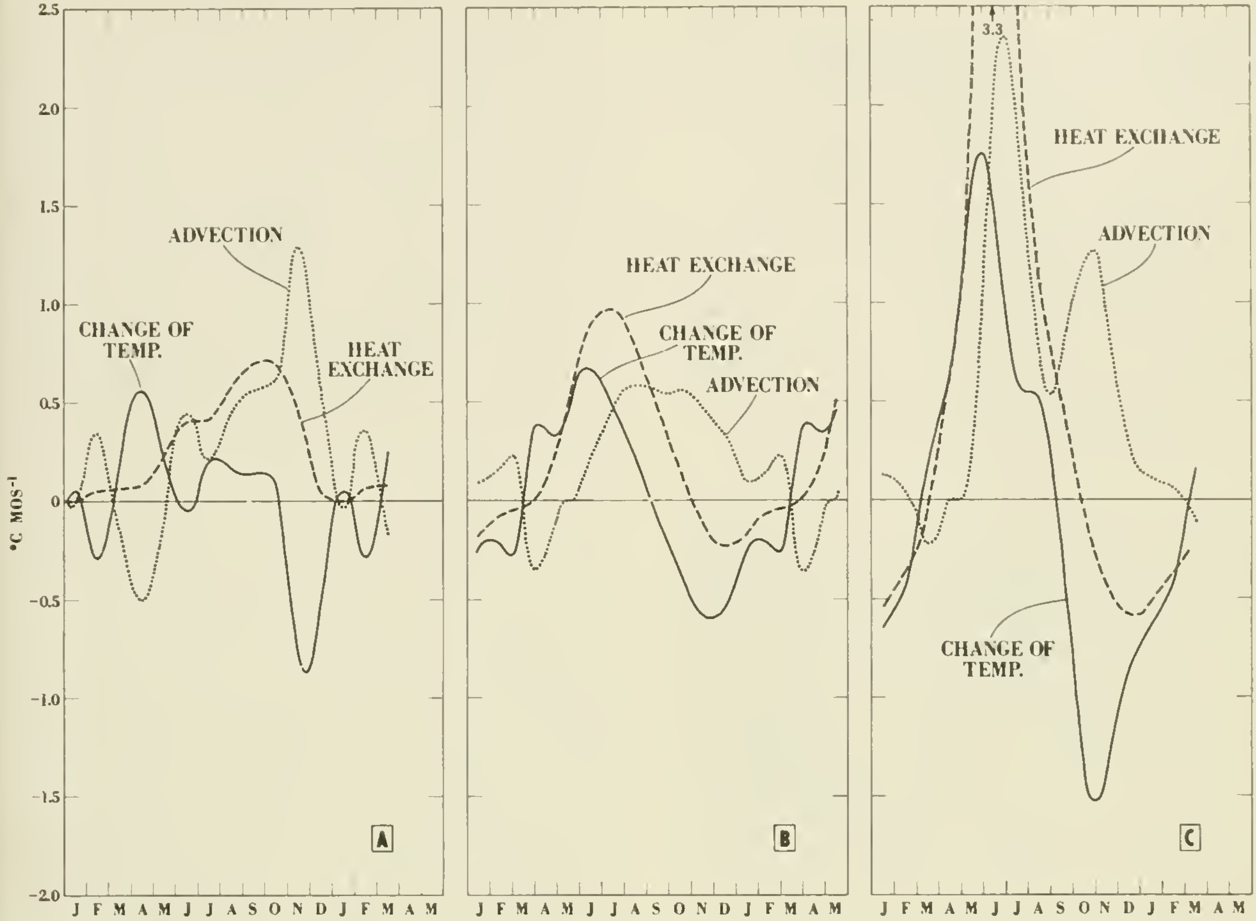


FIGURE 22.—Characteristic advection diagrams for the three-degree squares: A—14° to 17° N., 156° to 159° W.; B—20° to 23° N., 156° to 159° W.; and C—26° to 29° N., 156° to 159° W.

in December and January. It is also apparent that, during the summer, the change of temperature due to the heat exchange increases northward and, in winter, decreases northward (fig. 17).

South of the islands the maximum rate of temperature increase occurs in April and the maximum rate of decrease occurs in November and December. In the vicinity of the islands the time of maximum rate of increase has shifted to June, with the maximum rate of decrease occurring in November and December. To the north of the islands these maxima occur during May to June and October to November, respectively. Again, there are also changes in the magnitude of these extremes, which is particularly apparent to the north of the islands.

Together the $\frac{\Delta\theta}{\Delta t}$ and $\frac{H}{\rho c_p z}$ curves indicate advection and form combinations typical for their location. For example, during May in figure 22B and April in figure 22C, the two curves are superimposed or in phase for a brief period of time. This means that

$$\frac{H}{\rho c_p z}=\frac{\Delta\theta}{\Delta t}$$

and that there is no advection.

At other times, the heat exchange curve can be either above or below the temperature-change or heating curve, indicating either positive or negative advection, respectively. Positive advection means that colder water, and negative advection that warmer water, is moving into the area. In figure 22A and B, negative or warm advection occurs from March to May and positive, or cold advection, during the remainder of the year. This

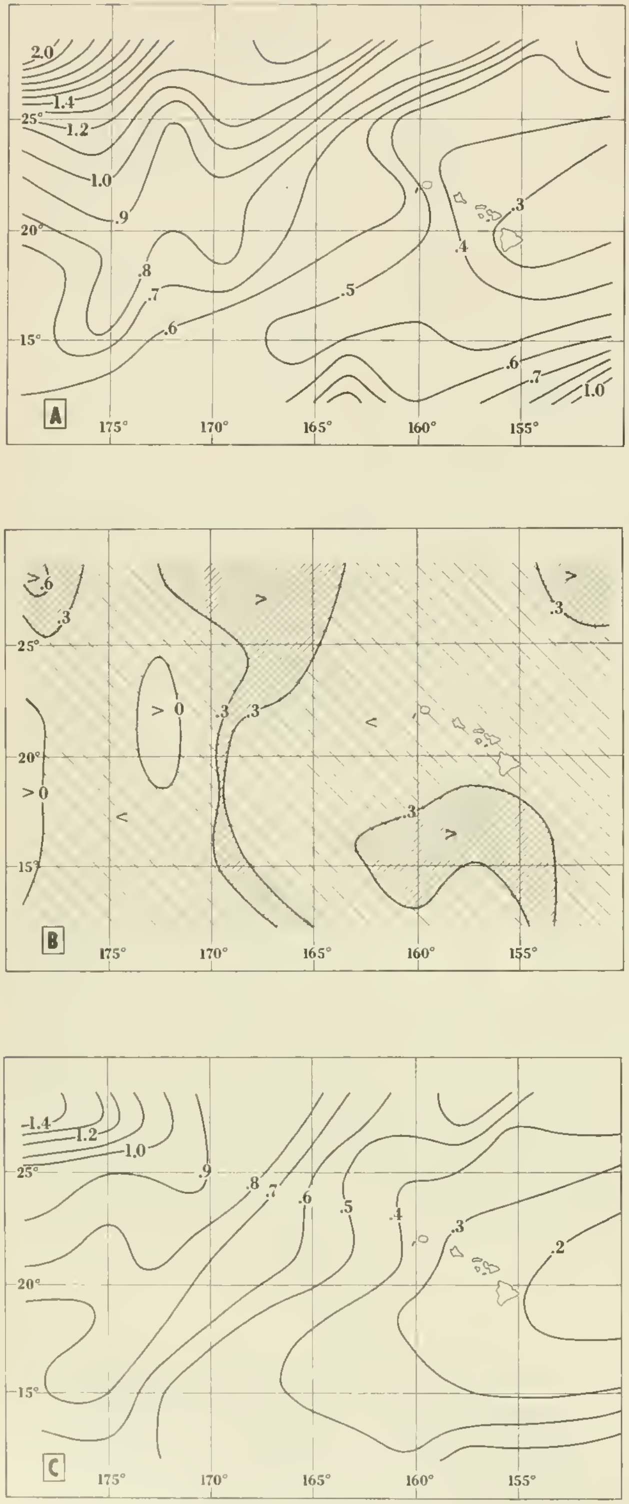


Figure 23.—Distribution of advection in the Hawaiian survey region (°C. mos.$^{-1}$). A—Mean positive (cold) advection; B—Mean negative (warm) advection; C—Mean annual advection.

is also true in figure 22C, except that negative advection is less pronounced and occurs earlier.

Phase differences between extremes of $\frac{H}{\rho c_p z}$ and $\frac{\Delta\theta}{\Delta t}$, and changing distances between these curves indicate a varying advention resulting in advection peaks. This is best illustrated by plotting the difference between $\frac{H}{\rho c_p z}$ and $\frac{\Delta\theta}{\Delta t}$ separately. North of the islands, for example, advection peaks occur in June to July and in October to November. To the south of the islands, advection peaks occur in February, June, and November. Within the island area, these peaks occur during February to March, August, and October.

Since both the $\frac{H}{\rho c_p z}$ and $\frac{\Delta\theta}{\Delta t}$ curves have shapes and times of maxima and minima typical for their location, one might call the $\frac{\Delta\theta}{\Delta t}$ curve, as may be obtained from an island monitoring station, a "characteristic heating curve." Similarly, the combinations of these curves form advection patterns typical for their location, so that curves, such as in figure 22, may be called "characteristic advection diagrams."

In order to explore the physical meaning of advection and discover its significance in the vicinity of the Hawaiian Islands, the region was divided into 60 three-degree squares for which characteristic advection diagrams were drawn. First, by measuring the area between $\frac{H}{\rho c_p z}$ and $\frac{\Delta\theta}{\Delta t}$ of each diagram, the mean positive, the mean negative, and the mean annual advection was obtained and their distribution plotted in figure 23.

Positive or cold advection occurs approximately from May to the following February and is distributed as shown in figure 23A. The feature of significance here is the trough of low advection extending southwestward from 21° N., 150° W., crossing the southern boundary of the region in the vicinity of 170° W. On both sides of the trough the mean advection increases to approximately 2° C. mos.$^{-1}$ in the northwest portion of the region and 1° C. mos.$^{-1}$ in the southeast.

Negative or warm advection occurs predominantly during March and April. Figure 23B shows that a distinct positive advection pattern is absent and that the magnitude ranges from 0 to 0.6° C. mos.$^{-1}$.

The short duration and low values of negative advection indicate that this is not important when the mean annual advection is considered. Figure 23C shows that the latter is positive throughout the region and reveals a distribution similar to that of the distribution of the mean positive advection. Although the trough of low positive advection has other implications, it is sufficient to note at this point that it may indicate a transition zone between two climatic regions, one in the southeast portion and the other in the northwest portion of the Hawaiian region.

The next step in the analysis involved grouping of the characteristic advection diagrams by similarity in shape and phase. Upon examination of the 60 diagrams, 2 primary, climatic regions became apparent. One is located in the northwest portion of the Hawaiian region (area A, fig. 24), with dominant positive advection during June and July and a secondary positive advection peak during December and January. The other climatic region is located in the southeast portion of the region (area B, fig. 24), with a dominant advection peak in October and November. The intermediate area is under the influence of both climates. The characteristic advection diagrams were then combined on the basis of climatic similarities and their number thus reduced to the nine presented in appendix B, chart V.

The diagram characteristic of area A shows a pronounced advection peak of 3.5° C. mos.$^{-1}$ in June, which then decreases rapidly until the end of November, except for a period of little change during October. A secondary advection peak of 1.1° C. mos.$^{-1}$ occurs during December and January and, finally, advection reaches a minimum of $-0.5°$ C. mos.$^{-1}$ during March.

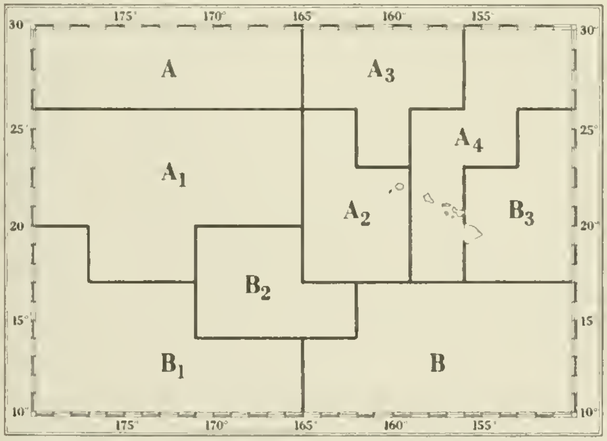


FIGURE 24.—Climatic areas of the Hawaiian region based on characteristic advection diagrams.

In area A_1, just south of area A, the June–July advection peak of 2° C. mos.$^{-1}$ and the secondary peak of 1.1° C. mos.$^{-1}$ in December–January are as pronounced as in area A, and, in addition, there is a secondary peak of 1.2° C. mos.$^{-1}$ in October. Area A_2, just to the west of the main islands, again exhibits these features: a primary peak of 1.2° C. mos.$^{-1}$ in June–July, a peak of 1° C. mos.$^{-1}$ in October–November and the third peak of 0.5° C. mos.$^{-1}$ in December–January. In area A_1, advection reaches a minimum of $-0.2°$ C. mos.$^{-1}$ in March and in area A_2 $-0.3°$ C. mos.$^{-1}$ in March–April.

In area A_3, east of area A, advection peaks of 2.1° C. mos.$^{-1}$ in June–July, of 1.1° C. mos.$^{-1}$ in September–October and of 0.7° C. mos.$^{-1}$ in November–December are present. A small advection peak also occurs in February–March, so that this, and the shift in the occurrence of the two secondary peaks, constitutes a departure from the periods of A, A_1, and A_2. One also notes that $\frac{H}{\rho c_p z}$ and $\frac{\Delta\theta}{\Delta t}$ are superimposed or in phase during May, as is also the case in area A_2, indicating a period of no advection during that month.

In area A_4, which extends from the northeast corner of the region through the main island group, the three pronounced advection peaks are again apparent. The main peak of 1° C. mos.$^{-1}$ has shifted to July–August. There is no phase shift in the October–November peak of 0.8° C. mos.$^{-1}$, and the February–March peak of area A_3 is now more pronounced at 0.5° C. per month. In addition, there appears a small peak during April–May. Minimum advection of $-0.7°$ C. mos.$^{-1}$ occurs in March–April.

If one regards the advection pattern of area A_1 as typical, then that of area A_2 shows only a slight change in shape, but no change in the time of advection peaks. In areas A_3 and A_4, one notes both a change in shape and phase shift of the advection peaks, which may be due to the barrier effects of the island chain within a varying current field.

The characteristic advection diagram of area B shows an advection peak of 1° C. mos.$^{-1}$ during

October–November and another, slightly lower, during August–September. Minimum advection of $-0.1°$ C. mos.$^{-1}$ occurs during April. The primary distinction between area B and the other areas of the region is the absence of both the June–July and the December–January advection peaks. The August–September advection period occurs in only two of the nine advection diagrams of this climatic area, leaving October–November as the important advection period of area B.

In area B_1, the southwestern portion of the region, the advection pattern appears more complex. Maximum advection of 1.1° C. mos.$^{-1}$ occurs in December–January, with a noticeable peak of 0.9° C. mos.$^{-1}$ in October–November and another distinct peak of 0.8° C. mos.$^{-1}$ in June–July. Minimum advection of $-0.2°$ C. mos.$^{-1}$ occurs during February.

Area B_2, north of areas B and B_1, has two pronounced advection peaks; one of 0.9° C. mos.$^{-1}$ in June–July and another of 1.1° C. mos.$^{-1}$ in December–January. Minimum advection of $-0.3°$ C. mos.$^{-1}$ occurs in March.

Finally, in area B_3, east of Hawaii, the advection pattern again appears more complex. Maximum advection of $>0.5°$ C. mos.$^{-1}$ occurs in October–November and, in addition, there are peaks of 0.5° C. mos.$^{-1}$ in July–August and December–January. Minimum advection of $-0.4°$ C. mos.$^{-1}$ occurs in March–April. In addition, there is an advection peak of 0.2° C. mos.$^{-1}$ in May–June, which is also apparent one month earlier in areas B_1, B_2, and A_4.

To summarize, the Hawaiian region was divided into areas on the basis of time of occurrence of positive advection peaks. In the northwest portion, a primary peak occurs during June–July and a secondary peak during December–January. In the southeast portion, the dominant peak occurs during October–November. The areas between exhibit varying magnitudes of these advection periods. Differences from the basic patterns in areas A_3, A_4, and B_3 may be due to varying effects of the island barrier in a changing current field. Negative advection, generally of small magnitude, peaked during March and April.

Since heat (temperature) advection is the scalar product of the current velocity and horizontal temperature gradient, it is difficult to visualize it as a water displacement perpendicular to an isotherm. In order to do so and to explore the physical significance of advection further, the intrinsic temperature and advection charts will be developed in the next section.

B. Intrinsic Temperature and the Heat Advection Chart

A measure of advection as obtained in the previous section can provide, if the horizontal temperature gradient is known, information only about the component of the current in the direction perpendicular to an isotherm. For example, if the advection is 1° C. mos.$^{-1}$ and the horizontal temperature gradient 1° C. per 60 miles, then this advection is equivalent to water shifting 60 miles perpendicular to the isotherm. If the gradient is 0.5° C. per 60 miles then the shift would be 120 miles.

Now assume that the surface temperature is conservative or an "intrinsic" property of a parcel of water. Then, as before, there would be no advection for currents parallel to an isotherm. However, a component of flow perpendicular to an isotherm, the temperature now being an intrinsic property of the water, would result in a shift of the isotherm. In other words, advection can be interpreted as a shift of "intrinsic" isotherms with the displacement distance depending upon the temperature gradient. An "intrinsic" isotherm, therefore, exhibits properties of a movable streamline or boundary in that there is no flow across the isotherm. Thus, no information can be gained about the flow parallel to an isotherm, but a component of flow perpendicular to the isotherm, using "intrinsic" temperatures, must result in a shift of the boundary or the "intrinsic" isotherm.

Although any intrinsic isotherm or salinity isopleth in the ocean is a movable boundary, the resulting advection due to their displacement is magnified in transition zones marked by higher temperature and (or) salinity gradients. Thus, the areas of high advection in the northwest and southeast portions of the Hawaiian region (fig. 23) can be interpreted as transition zones, with moving boundaries, between climatic regions. These climatic regions were recognized by the characteristic advection diagrams of areas A and B in the previous section. Areas of high salt advection due to boundary movement are also to be expected during summer at 21° to 23° N., 155° to 160° W., and during fall at 13° N., 155° to 160° W., on the basis of high salinity gradients shown in figures 10 and 9, respectively.

The foregoing discussion can be further illustrated by computing intrinsic temperatures with the help of the simplified heat budget, equation 6.

Since only two processes, the heat exchange across the sea surface and advection, are assumed to contribute to the change of temperature, one can compute what the change of temperature should be if there were no heat exchange. The heat budget equation

$$\frac{\Delta\theta}{\Delta t}=\frac{H}{\rho c_p z}-\overline{V}\cdot\nabla\theta$$

then becomes

$$\left.\frac{\Delta\theta}{\Delta t}\right]_a=-\overline{V}\cdot\nabla\theta,$$

the change of temperature due to advection only.

Considering the unit of time to be one month, one can compute the intrinsic temperature, θ_I, at the end of a month for any location, if that month's advection is known, from

$$\theta_I-\theta_1=-\overline{V}\cdot\nabla\theta \text{ or}$$

$$\theta_I=\theta_1-\overline{V}\cdot\nabla\theta$$

where θ_1 is the temperature at the beginning of the month. One can also obtain the intrinsic temperature by subtracting the net heat exchange during a month from the temperature at the end of the month:

$$\theta_I=\theta_2-\frac{H}{\rho c_p z}.$$

A chart of the temperature distribution at the beginning of the month and one for the intrinsic temperature at the end of the month can now be drawn and combined. This new chart then illustrates advection in terms of the displacement of intrinsic isotherms or boundaries.

For the Hawaiian region, four "advection charts" were prepared (chart VI, appendix B), one each for the three advection periods, June–July, October–November, and December–January, and one for the minimum or negative (warm) advection period of March–April.

In the first chart the solid and dashed isotherms show the mean temperature distribution for the beginning of March and April and the mean intrinsic temperature distribution for the end of March and April, respectively. The chart shows that the displacement of the intrinsic isotherm is small throughout most of the region and probably not significant. The 24° and 25° C. isotherms are displaced northward, however, by as much as 180 miles in the eastern portion of the region, indicating warm advection.

The March–April advection chart therefore indicates either no current flow, or currents parallel to the isotherms, with some warm advection in the eastern portion. This is compatible with the gross winter geopotential topography (chart IV), which indicates little flow in the northern half of the region and flow parallel to the isotherms in the southern half.

The June–July advection diagram shows the average isotherms for the beginning of these months slope from northwest to southeast, whereas the average intrinsic isotherms for the end of these months, except for the southwest portion, show an east-west direction. Thus, this advection chart for the principal advection period shows very little displacement of the 25° and 26° C. isotherms in the eastern portion of the region, whereas in the western portion displacement may be as high as 550 miles per month, indicating a southward component of flow of 0.7 to 0.8 knot. Although there are insufficient current data to compute the advection independently, a westerly setting current of 1 knot could accomplish this displacement. High advection is also indicated in the northern portion of the region, where the displacement increases westward from 150 miles per month to more than 500 miles per month.

This advection chart conveys a picture compatible with salinity changes if one postulates water entering the survey region from the east and pushing the intrinsic isotherms southward as if they were movable boundaries. The water entering the survey region from the east also decreases the salinity in the vicinity of the Hawaiian Islands during the spring, reaching a minimum in July (fig. 9), despite the fact that this is a period of maximum evaporation minus precipitation (fig. 20).

High heat advection in the vicinity of Midway Island during June and July is also compatible with the sharp salinity decline during those months (fig. 9).

The characteristic advection diagrams of the previous section (chart V) show that the advection declines after the primary peak in June–July, but then rises again in August or September to reach a secondary peak in October–November. The advection chart for the October–November period shows no material difference between the mean isotherm pattern for the beginning of these months and the mean intrinsic isotherm pattern for the end of these months. High advection continued in the western half of the region, with the principal change from the previous chart occurring in the southeast portion. There advection was low during the June–July period and then increased to 1° C. mos.^{-1} in October, as shown in the characteristic advection diagram of area B (chart V).

The displacement speeds of the 26° and 27° C. isotherm in the southern portion of the region are as high as 0.9 knot, in the northwest portion they are about 0.5 knot and, in the northeast portion the 25° isotherm was displaced at a speed of about 0.2 knot.

To explain this advection picture one can postulate that the westerly flow of the June–July period slackened and shifted to the southeast portion of the region. This is coincident with the intrusion of lower salinity water into that area, as indicated in figure 9 showing the seasonal salinity variation at 13° N. One can further postulate that with the relaxation and southward shift of the flow from the east, higher salinity water from the northwest reoccupies the region from which it had been displaced during the primary advection period. This, again, is in agreement with the salinity data as shown in figure 8.

The final advection period, as indicated by the characteristic advection diagrams, occurs during December and January in all the areas except in area A_4 where it is delayed until February and area B where it is absent. The mean temperature for December and January at the beginning of these months, and the mean intrinsic temperature for the end of these months are beginning to assume the distribution of the March–April period. The chart shows displacements of the 25° and 26° C. isotherms in the central portion of the region of up to 360 miles or at a rate of about 0.5 knot. To the north, the 24° C. isotherm is displaced by up to 120 miles or at a rate of less than 0.2 knot.

The primary advection during June and July can be associated with an intensification of the tradewind system and the secondary period during October and November with its relaxation. However, there appears no wind pattern which could be associated with the December–January advection peak. In the vicinity of the main Hawaiian Islands the salinity reaches a peak during the December to February period and northeast of the Marshall Islands the horizontal temperature distribution at 400 ft. (Robinson, 1954) suggests intensified circulation. This points to an inertial surge in the high salinity circulation system as the explanation for the advection peak.

Although the water movement as suggested by the advection periods has not been observed directly, present knowledge of the general Pacific circulation, and the sketchy salinity data, are compatible with the advection model. In the next section, therefore, it will be shown that the surface temperature can be used to monitor physical processes.

C. Characteristic Heating Curve

The simplified heat budget, equation 6, shows the rate of change of temperature to be a function of the two independent variables; the heat exchange across the sea surface and the heat advection. Since the seasonal variation of the heat exchange across the sea surface and the seasonal variation of the advection are characteristic of the oceanographic climate at any location, the dependent, seasonal variation in the rate of change of temperature should also be characteristic of the location. A graph of the seasonal rate of change of temperature can therefore be called the characteristic rate of change temperature curve, or, simply, the "characteristic heating curve."

The characteristic advection diagrams of chart V show, with the exception of areas B and B_1, that the heat exchange curves have a regular seasonal shape, with a maximum in June and a minimum in December or January. Changes in advection should therefore be reflected in irregularities of the characteristic heating curves. For example, in April the change of slope in the characteristic heating curve of most areas in the survey region (chart V) indicates a change from negative (warm) advection to positive (cold) advection. In the northeastern portion of the survey region (areas A_4 and B_3), the pronounced dip in the characteristic heating curve during April and May signifies an initial surge of cold advection, which then slackens during May and June, as indicated by the rapid rise of the rate of change of temperature.

Again, in most areas of the survey region, the rapid decline in the characteristic curve, after reaching a peak in May–June, is associated with the June–July advection peak. The slackening of the primary advection is reflected in a change of slope in the characteristic heating curve or a secondary peak as in areas A_2, A_3, A_4.

In areas A, A_1, A_2, A_4, and B_3, both the October–November and the December–January (February for A_4) dips in the characteristic heating curves can be interpreted as advection peaks at those times. In areas B_1 and B_2, these advection periods overlap in such a way as to produce only a single minimum in the characteristic heating curve.

Generally, the characteristic heating curve is expected to be sensitive to cold advection during a period of rising heat exchange and most sensitive to warm advection during declining heat exchange. During the winter months in areas where heat exchange is small, the characteristic heating (cooling) curves would be very sensitive to changes in advection. This is illustrated in the characteristic advection diagram of area A_1, where the secondary advection peaks produce large changes in the characteristic heating curves during October–November and December–January.

The characteristic advection diagrams of chart V are useful in discovering gross climatic features and in delineating climatic regions. More useful, however, are the characteristic heating curves drawn from data regularly collected at fixed monitoring stations, particularly if features of the curve can be related to other continuously monitored events or processes. Gross climatic processes, as discovered in the characteristic advection curves, should again be reflected in the shape of the heating curves.

Figure 25 represents the characteristic heating curve as drawn from mean data collected in the vicinity of Koko Head, Oahu, from 1951 to 1958. It differs from that of figure 22B primarily during the winter months, when it forms only one minimum in December, whereas the latter forms a minimum in November–December and another dip in the characteristic temperature curve during January–February. The March–April and the June peaks are in phase on both diagrams. These differences are to be expected, since the curve of figure 22B represents data collected in a three-degree square covering both sides of the island chain. The Koko Head curve, on the other hand, represents data collected only at a point on the "island barrier" within a large circulation system.

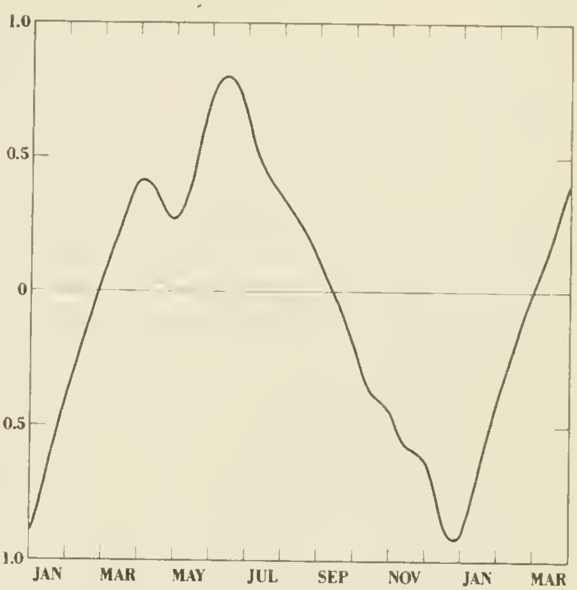


FIGURE 25.—Mean (1951–58) characteristic heating curve for the vicinity of Koko Head, Oahu.

The mean characteristic heating curve at Oahu, then, shows that the rate of change of temperature becomes positive at the end of February, indicating warm advection. The commencement time is similar to that in area A_2, just to the west of Oahu. The rapid rise in the rate of change of temperature during May can be interpreted as a period of low advection, as in figure 22B where the rate of change of temperature is the same as the net heat exchange across the sea surface. Since, during this time of the year, the isotherms are approximately parallel to the islands (see May temperature chart II), this means that the flow is also parallel to the island chain. Then, again as in figure 22B, the rate of change of temperature reaches its maximum in June, slightly later than in area A_2 and earlier than in area B_3. This is also apparent in area A_4, where a combination of maximum rates of change of temperatures occurring either during May–June or June–July produce the wide peak in the characteristic heating curve.

Since the flow during the June–July advection period is from east to west, at a low angle of incidence within the island chain, one can postulate that its deflecting effect is at a maximum. However, as the incident flow acquires a southerly component and the angle between it and the island

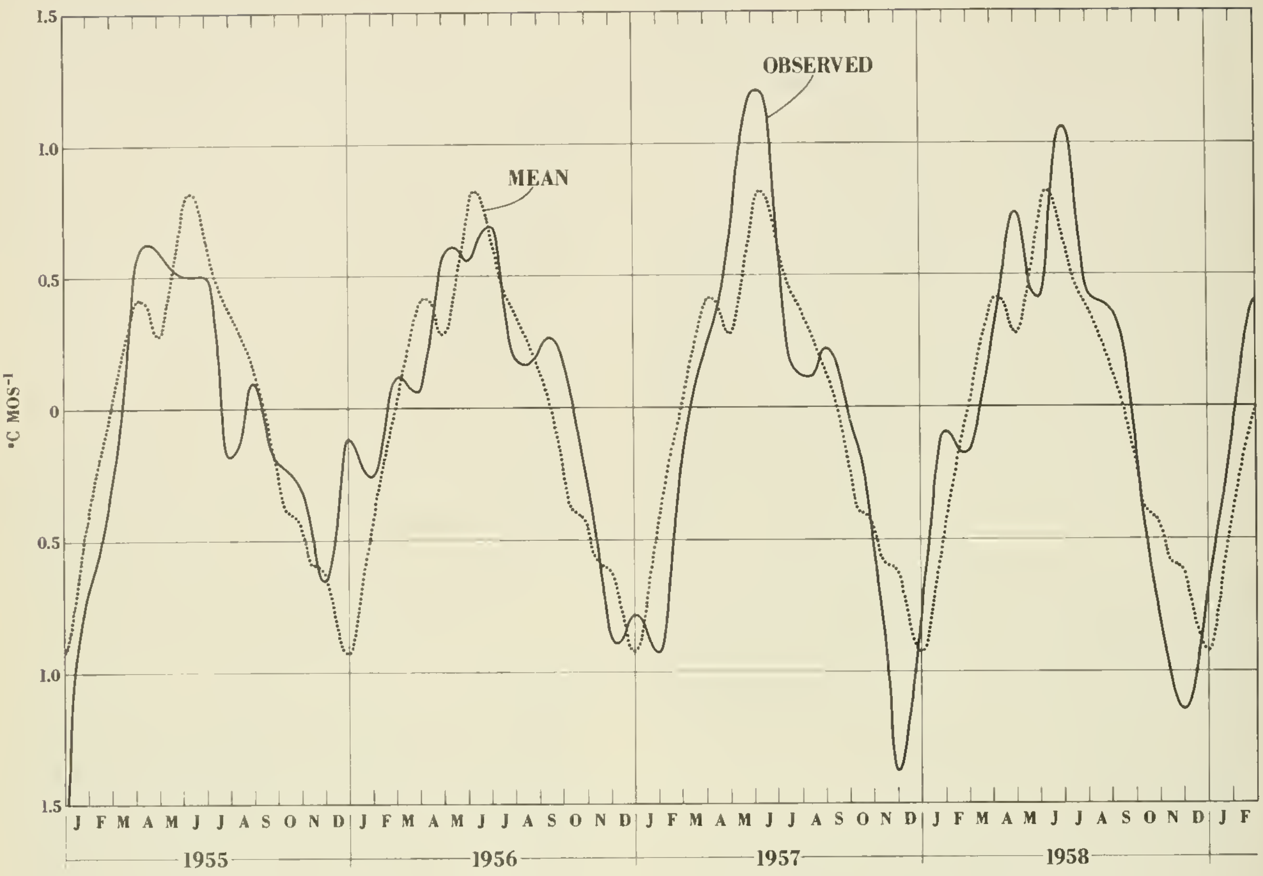


FIGURE 26.—Characteristic heating curve at Koko Head, Oahu, 1955 through 1958.

chain becomes larger, water will pass through the channels and cold advection becomes apparent. This has the effect of delaying and damping the June–July advection so as to merge it with the October–November period, as is indicated in the advection curve of figure 22B. The advection diagram of area A_4 does not exhibit this feature, since it is a combination of diagrams primarily of the northeast portion of the region, where the June–July advection peak is delayed but not damped out.

Finally, the characteristic heating curve for Oahu reaches a minimum during December, indicating that the December–January advection peak is affecting this area, rather than the delayed February peak to the northeast of the islands.

Figure 26, showing the rate of change of temperature of the Koko Head (Oahu) monitoring station from 1955 through 1958, further illustrates the utility of characteristic heating curves. Here the dashed line represents the mean characteristic curve discussed above and the solid line, the observed data. Pronounced deviations from the mean characteristic curve are apparent during 1955 and 1957. In 1955, the maximum rate of change of temperature occurred during April and then decreased irregularly to reach its minimum during November–December. The early peak and the generally decreasing trend in the rate of change of temperature are comparable to curves found south of the islands, such as in figure 22A for the three-degree square 14° to 17° N., 156° to 159° W.

Similarly, the shape of the characteristic heating curve in 1957, with a peak 0.4° C. mos.$^{-1}$ higher than the mean peak, resembles curves found north of the islands, such as in figure 22C for the three-degree square 26° to 29° N., 156° to 159° W. In short, since the shape of the characteristic heating curves reflects the oceanographic climate, one can say that, during 1955, Oahu was located within an oceanographic climate normally to be found to the south, and, during 1957, Oahu was located within an oceanographic climate normally to be found to the north.

During 1956, the dip in the heating curve which signals the end of the warm advection period occurred during March–April, approximately one month earlier than in the mean curve. The significance of two peaks during the May to July period rather than one as in the mean Koko Head curve is not apparent. The dip in the heating curve during August of 1956 to below and, subsequently, to above the mean curve can be interpreted as more pronounced cold advection.

From March to October 1958, the shape of the heating curve resembled the mean curve except that the March–April peak, the April–May dip, and the June peak, occurred approximately one month later.

During the autumn and winter months from October 1955 to March 1958, the dual dips in the heating curve are as apparent as in figure 22C. They reflect the cold advection peaks of November–December and January–February, and in each case deviate from the mean Koko Head curve.

Thus, certain changes in the surface temperature can be interpreted in terms of physical processes. Figure 26 also shows that deviations from the mean characteristic heating curve can be large, exhibiting features which can be found in the characteristic curves of adjacent areas.

Before closing the discussion on heat advection, the validity of the results will be examined. Although shapes of curves and times of advection peaks and dips in the rate of change of temperature were stressed, it is useful to review the magnitude of advection encountered. In the previous section displacement velocities of up to one knot were calculated, which seem high for the mean conditions discussed here. However, on the basis of the assumption used in the derivation of the simplified heat budget, high advection values are to be expected. First, it is probable that the actual depth through which heat is distributed, or the "effective" mixed layer, is greater than the measured mixed layer so that the computed heat exchange in terms of temperature change, $\frac{H}{\rho c_p z}$, would therefore be too high and result in excessive heat advection. Neglecting the effects of diffusion in the simplified heat budget equation would also tend to increase the computed advection.

The assumptions, then, would affect the magnitude of advection, but not necessarily the advection periods. This view is supported by the consistency of the advection periods throughout the survey region, despite data of less than desirable quality.

In the discussion of the characteristic heating curves obtained from the Oahu monitoring station (fig. 26), deviations of the rate change of temperature from the mean were explained in terms of advection. This implies that year-to-year changes in the heat exchange and diffusion are insufficient to account for these deviations.

In the vicinity of the Hawaiian Islands, examination of the vertical temperature gradient below the mixed surface layer suggests that the stability remains relatively constant throughout the year. Significant changes in the vertical diffusion are therefore unlikely, even though diffusion may not be negligible in heat budget considerations. The calculated heat losses from the sea surface (evaporation, back radiation, and conduction of sensible heat) seasonally vary by about 5 percent. On a year-to-year basis, then, the variation of these heat losses would probably be less than 5 percent.

Remaining is the incident radiation at the sea surface which, due to cloud cover, can vary considerably. Maximum deviations in the characteristic heating curve due to this cause would occur during May, June, and July, when insolation is at a maximum and the depth of mixed layer is at a minimum. To estimate reasonable deviations, assume that the year-to-year variation in the mean monthly cloud cover is less than the seasonal range of one tenth. On this basis, deviations of less than 0.2° C. mos.$^{-1}$ in June and less than 0.1° C. mos.$^{-1}$ in December can be expected.

Deviations from the mean characteristic heating curves in figure 26, which were interpreted in terms of advective changes, were as follows:

April 1955	+0.25° C. mos.$^{-1}$
June 1955	−0.3° C. mos.$^{-1}$
December 1955–January 1956	+0.8° C. mos.$^{-1}$
March–April 1956	−0.3° C. mos.$^{-1}$
September 1956	+0.2° C. mos.$^{-1}$

October 1956	+0.35° C. mos.$^{-1}$
November–December 1956	−0.2° C. mos.$^{-1}$
January–February 1957	−0.5° C. mos.$^{-1}$
June 1957	+0.4° C. mos.$^{-1}$
November–December 1957	−0.7° C. mos.$^{-1}$
April–May 1958	+0.4° C. mos.$^{-1}$
June–July 1958	+0.3° C. mos.$^{-1}$
November–December 1958	−0.45° C. mos.$^{-1}$

These are all in excess of changes to be expected from the assumed year-to-year variations in the net heat exchange.

PART III. OCEANOGRAPHIC CLIMATE OF THE HAWAIIAN ISLANDS REGION

In the first section of this atlas, the distribution of surface variables and their gross seasonal changes in an area bounded by 10° N., 30° N., 150° W., and 180°, were described. These consisted of surface temperatures, salinities, depths of the mixed layer, and dynamic heights. In the second section, the changes of surface variables were studied in terms of physical processes, such as the net heat exchange across the sea surface and advection.

In this final section, an attempt will be made to use the results of the first two sections to construct a climatic model of the Hawaiian region. This, of necessity, will only be a first approximation, since none of the data used here were collected for purposes of a climatic study. This first approximation, however, may be of use in designing experiments to correct and improve the climatic model.

The currents and water masses of the North Pacific were described by Sverdrup et al. (1942, ch. XV). They defined the Subarctic Pacific water mass, the Eastern and the Western North Pacific Central water mass, and the Pacific Equatorial water mass on the basis of temperature-salinity relations below the surface layer. Approximately associated with these subsurface water masses one also finds surface water types. These are the Subarctic Pacific Water type, the North Pacific Central Water type, and the North Pacific Equatorial Water type as illustrated in figure 27. On the basis of Schott's (1935) temperature and salinity charts, the Subarctic Pacific type would be cold and have a salinity of 33‰ or less, the North Pacific Central type would be warm and have 35‰ or more, and the North Pacific Equatorial type would be warm and have about 34‰ or less. The chief distinction between water types and masses is that the former are under the direct influence of the physical processes taking place at the sea surface, whereas the latter are not. One would therefore expect relatively large seasonal

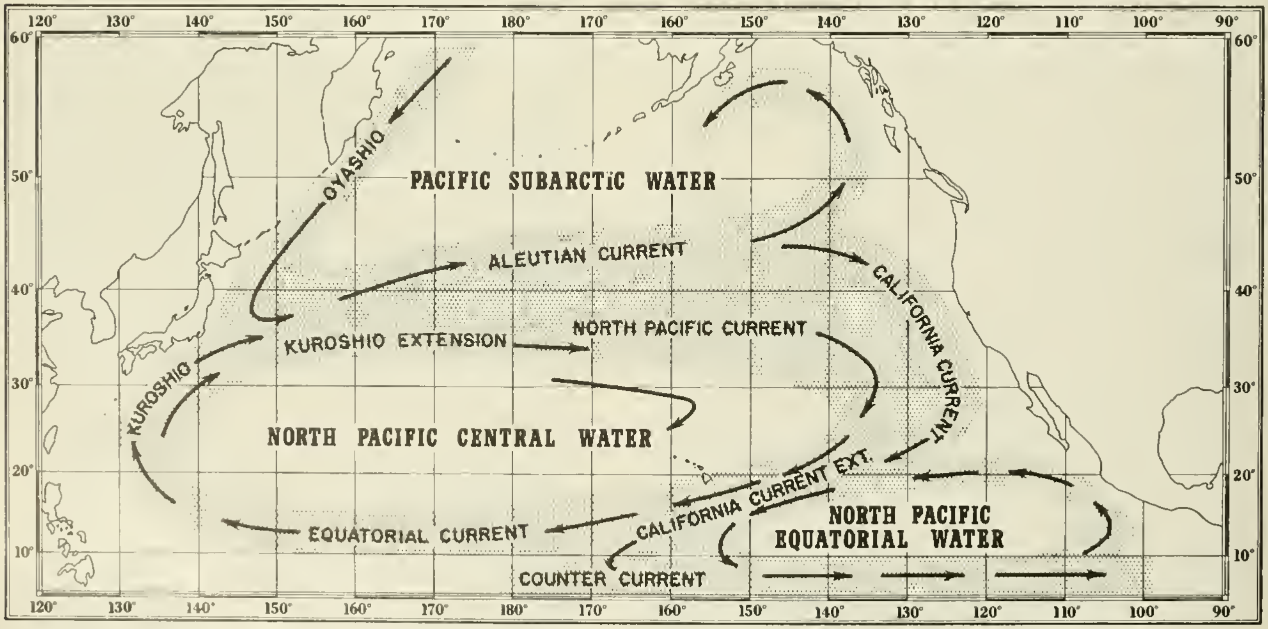


FIGURE 27.—A schematic chart showing the major North Pacific water types and currents.

temperature and salinity changes in the surface water types. The position of their boundaries would also be subject to changing wind stresses, so that they would not always coincide with the corresponding water-mass boundaries.

The water types mentioned also form centers of the large circulation systems of the North Pacific, since one finds the major ocean currents on their periphery. Thus, the currents are located in the transition zones between the principal water types and one would expect this to be reflected in the changing composition of the water as it flows across the Pacific. For example, a parcel of water starting in the Kuroshio would be mixed with water from the Oyashio and then in its passage across the Pacific acquire new chemical characteristics during possibly two or three seasons of winter overturn. Then, this parcel of water would be further modified, first in the California Current by American coastal water and later, in the California Current Extension, by North Pacific Equatorial water. Finally, southeast of the Hawaiian Islands, one would expect its chemical composition to differ from both its original composition in the Kuroshio and from that of the North Pacific Central Water.

This, of course, is supposition, since no supporting measurements of chemical tracers are available. However, the relatively high salinity gradient at 35‰ in the vicinity of the Hawaiian Islands (fig. 10) can be interpreted as the boundary between the Western North Pacific Water and the transition water called here the California Current Extension.

The oceanographic environment of the Hawaiian Islands, therefore, corresponds with that described by Sverdrup et al. (1942), except that they based their analysis on a study of water masses, in contrast to the water types considered here. Thus, on the basis of Schott's (1935) temperature charts, the North Pacific Equatorial water type is distinct from the South Pacific Equatorial type.

Sverdrup et al. also distinguish between the Eastern North Pacific and the Western North Pacific Central water mass. Surface salinity data for the November to February period (chart III) show only a single high salinity cell to extend eastward across the northern portion of the region and, on the basis of winter data collected on *Hugh M. Smith* cruise 25 (McGary, 1956), there is no evidence of an Eastern North Pacific cell. The April to August surface salinities (chart III) show two high salinity cells in the northern portion of the area. This can be explained as a separation of the single, winter cell caused by the deflecting effect of the island chain on a westward setting current. The surface water in the two high salinity cells is therefore believed to be of the North Pacific Central type.

New information to be added to this general picture is concerned with the three types of boundaries described in part I. First, there was the boundary separating areas in which the times of maximum and minimum depths of mixed layer differed (fig. 3). This is also coincided with the node at 15° N. (fig. 2) and the associated, seasonal displacement of the depth of mixed layer trough (chart I). Then there was a boundary at about 18° N. south of which the seasonal temperature range remained relatively constant and north of which it increased rapidly northward (fig. 5). The relatively high salinity gradient of figure 10, moving seasonally through the Hawaiian Islands, was identified as the third type of boundary separating two types of water.

In order to interpret these features, a simplified heat budget was formulated in part II. This related the rate of change of surface temperature with the processes of net heat exchange across the sea surface and advection. The meridional profiles of figures 17 and 18 revealed a boundary south of which the net heat exchange across the sea surface was positive throughout the year and north of which it was positive during the summer and negative during the winter. The boundary, located at about 18° N., coincided approximately with the temperature boundary. The meridional distribution of the net heat exchange across the sea surface therefore appears to be associated with the seasonal changes in the meridional temperature distribution described in part I.

On the basis of the net heat exchange (fig. 15), one would also expect maximum and minimum sea surface temperatures to be reached in November and April, respectively. Figure 7 shows that the maximum temperature at 20° N. is reached in September and the minimum in March, illustrating that these times are primarily determined by the net heat exchange across the sea surface. However, particularly in autumn, there is an important phase difference attributable to advection.

Since no direct measurements of this term were available, it was estimated by subtracting the rate of change of surface temperature from the rate of change of temperature caused by the net heat exchange across the sea surface. The advection can also be obtained graphically by measuring the difference between the seasonal rate of change of the temperature curve and the seasonal heat exchange curve, as in the advection diagrams of figure 22. This method was applied to three-degree square areas in the Hawaii region and revealed four distinct advection periods. The first period during March and April was one of low or warm advection and the others were periods of cold advection during June-July, October–November, and December–January.

The advection diagrams also suggested different climatic zones. In the northwest portion of the region, area A of chart V, the primary advection peak occurs during June–July and a secondary peak during December–January. In the southeast portion of the survey region, area B of chart V, the primary advection peak occurs during October-November and the June–July and December-January periods are absent. In the intermediate areas the diagrams of chart V exhibit varying magnitudes of these advection peaks, which suggest a transition from one to the other climatic zones. Area B also corresponds approximately with the area south of the depth of mixed layer boundary in which the times of maximum and minimum depths differed from those to the north. Thus, the depth of mixed layer boundary and the advection peaks appear to be closely associated with seasonal changes in water motion.

In order to illustrate the physical meaning of heat advection, the change of temperature caused by advection can be added to the temperature at the beginning of the month in order to obtain the "intrinsic" temperature at the end of the month. If the two temperature distributions are then plotted on the same chart, the displacements of isotherms are then equivalent to boundary movements, as shown in chart VI, for the four advection periods in the Hawaii region. Of particular importance are the June–July and October–November charts, since the independently observed salinity changes mentioned above both support and supplement the information obtained from heat budget considerations. First, within the island area, the June–July advection period coincides with the northward motion of the salinity boundary and the declining salinity which reaches a minimum in July. Later, the October–November heat advection period coincides with the southward retreating salinity boundary and increasing salinity within the islands. In addition, the October–November advection peak in the southeast portion of the survey region coincides with the rapid salinity decline at 13° N. The salinity decline at 21° N. and at 13° N. can only be explained by salt advection, since, at 21° N., evaporation minus precipitation is positive throughout the year and increasingly positive at 13° N. during November (fig. 19).

The displacement of the 26° C. "intrinsic" isotherm and the spring and autumn movement of the salinity boundaries as indicated by the 35 °/₀₀ and 34 °/₀₀ isopleths are illustrated in figure 28. The June–July displacements (fig. 28A) are best explained by an intensified westward component of flow between 15° and 25° N. The October–November displacements (fig. 28B) are best explained by an intensified southward component of flow in the northern half of the region, and an intensified westward component of flow in the southeastern portion.

It is now apparent that the trough of low advection during the cold advection period in figure 23A is associated with the transition zone between two climatic regions. In addition, one can postulate that the trough coincides with the core of the California Current Extension and that the areas of high advection on both sides of the trough are the areas of the seasonally moving current boundaries. The latter can also be expressed as the areas through which the boundaries of the seasonally dilating and contracting North Pacific Central and North Pacific Equatorial systems move.

The surface temperature distribution and its seasonal changes primarily reflect the seasonal changes in the heat exchange across the sea surface. Features in the temperature distribution which may be due to the surface circulation are therefore obscured, except for the tongue-shaped area of lower temperature protruding westward south of the islands during the summer months (chart II), reflecting the increased westward flow.

The surface salinity distribution, on the other hand, appears to be more closely related to the

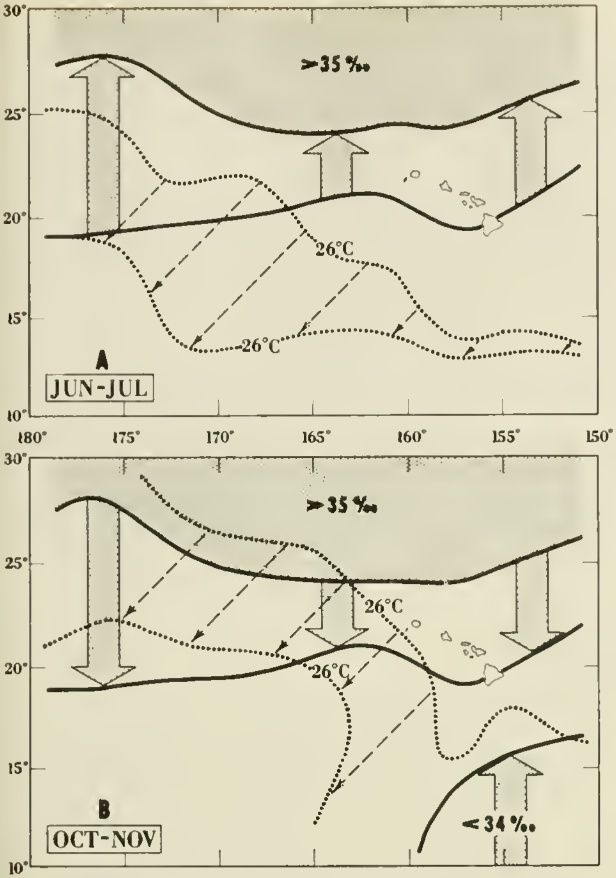


Figure 28.—Advection charts: A. Displacement of the June–July 26° C. "intrinsic" isotherm and schematic spring displacement of the 35°/oo isopleth. B. Displacement of the October–November 26° C. "intrinsic" isotherm and schematic autumn displacement of the 35°/oo and 34°/oo isopleths.

circulation systems. This can be explained by the fact that since the Hawaii region is neither one of extreme evaporation nor precipitation, the surface salinity is affected less by evaporation minus precipitation than the temperature is by the heat exchange. In other words, in the Hawaii region the surface salinity is less "non-conservative" than the temperature. The salinity boundary passing seasonally through the islands is therefore not obscured by the events at the sea surface, which is the case with an "intrinsic" temperature boundary that would exist between the Western North Pacific water and the California Current Extension. Of course, faint traces of a temperature boundary similar to the salinity boundary were noted in the zonal temperature distribution (fig. 6).

The seasonal variations in the heat advection appear to be closely related to climatic features in the distribution of the surface depth of mixed layer which probably reflect changes in the wind stresses at the sea surface. Advective peaks also coincide with changes in salinity which must be attributed to salt advection. The temperature and salinity gradients, however, differ both in magnitude and direction, so that one would not expect isopleths of salinity to move in the same direction as the isotherms (fig. 28).

It is now possible to add seasonal, climatic changes to the circulation model which was schematically illustrated in figure 27. During spring and early summer, the California Current system intensifies and as a result the California Current Extension spreads and displaces the North Pacific Central water within the Hawaiian Islands. The peak displacement of this water, as illustrated by the 35°/oo isopleth in figure 8, is reached during July and coincides with the June–July heat advection peak. In late summer and early autumn, as the California Current system weakens, the transition type of water of the California Current Extension retreats and is again replaced by the higher salinity North Pacific Central type of water. This movement of the boundary between the two types of water is associated with the October–November head advection peak. Concurrently with the weakening of the California Current system, North Pacific Equatorial water spreads into the southeast portion of the survey region, as reflected both in the sharp salinity decline and the major October–November heat advection peak for that area.

During this period the surface temperature charts also show a counterclockwise rotation of the tongue-shaped lower temperature water south of the islands from the July position to the November position (chart II). In addition, there is an appearent southward displacement of the depth of the mixed layer boundary in the western portion of the region. These features can be interpreted to mean that, as the California Current Extension weakens, its recirculation into the Countercurrent shifts from west of 175° W. to between 160° and 170° W.

In the Hawaii region the February to April period appears to be one of relaxation. In the northern half, the parallel structure of isotherms probably reflects negligible net current motion, as is also indicated in the winter geostrophic current chart (chart IV). In the southern half, the flow is probably parallel to the isotherms.

The picture, therefore, is one of dilation and contraction of the North Pacific Central and the North Pacific Equatorial systems associated with the seasonal variation in the intensity and position of the surface currents.

This model can be monitored by means of a "characteristic heating curve," which is produced simply by plotting the rate of change of surface temperature at any given location. The curve for Koko Head, Oahu (fig. 20) showed, for example, that in 1955 the North Pacific Central system near Hawaii was displaced northward, and in 1957 southward. Varied magnitudes and displacements in the characteristic fluctuations of the curve reflected changes both in the intensity and time of the advection periods.

Returning to the original motivation for this climatic study, one finds that the Hawaii skipjack season coincides with the period from April or May to September or October, when the boundary of the North Pacific Central types of water passes Oahu in its northward and southward motion, respectively. This may mean that the availability of skipjack is associated with either the transition water of the California Current Extension and (or) a dynamic effect which is produced when this current enters the island area.

In conclusion, Gosline and Brock (1960:21) state that none of the Hawaii inshore fishes have come from the North American coast. This provides independent support for the climatic model according to which the Hawaii archipelago is predominantly bathed by North Pacific Central water.

LITERATURE CITED

Albrecht, F.
1951. A. Monatskarten des Niederschlages im Indischen und Stillen Ozean.
B. Monatskarten der Verdunstung und des Wasserhaushaltes des Indischen und Stillen Ozeans. Berichte des Deutschen Wetterdienstes in der U.S.-Zone No. 29. 39 p.

Austin, T. S.
1954. Mid-Pacific oceanography Part V, Transequatorial waters, May-June 1952, August 1952. U.S. Fish and Wildlife Service, Special Scientific Report—Fisheries No. 136. 86 p.
1957. Summary, oceanographic and fishery data, Marquesas Islands area, August-September 1956 (EQUAPAC). U.S. Fish and Wildlife Service, Special Scientific Report—Fisheries No. 217. 186 p.

Bruneau, L., N. G. Jerlov, and F. F. Koczy.
1953. Physical and chemical methods. Appendix: Table 1. Physical and chemical data. Reports of the Swedish deep-sea expedition 1947–48, vol. III, fasc. II.

Cromwell, T.
1951. Mid-Pacific oceanography, January through March 1950. U.S. Fish and Wildlife Service, Special Scientific Report—Fisheries No. 54. 9 p.

Cromwell, T. and T. S. Austin.
1954. Mid-Pacific oceanography II, by T. Cromwell, and Mid-Pacific oceanography III, by T. S. Austin. U.S. Fish and Wildlife Service, Special Scientific Report—Fisheries No. 131. (Part II, 13 p.; Part III, 17 p.)

Fleming, J. A., C. C. Ennis, H. V. Sverdrup, S. L. Seaton, and W. C. Hendrix.
1945. Scientific results of cruise VII of the Carnegie during 1928–1929 under command of Captain J. P. Ault. Oceanography-I-B, Observations and results in Physical Oceanography. Carnegie Institution of Washington, publication 545. 315 p.

Gosline, W. A. and V. E. Brock.
1960. Handbook of Hawaiian Fishes. University of Hawaii Press, Honolulu. 372 p.

Holtsmark, B. F.
1949. Final report: the SOFAR project: Hawaiian oceanographic survey, USS *Fieberling*, February to July 1947. Report 139, U.S. Navy Electronic Laboratory, San Diego. 58 p.

Jacobs, W. C.
1951. The energy exchange between sea and atmosphere and some of its consequences. Bulletin of the Scripps Institution of Oceanography, vol. 6, No. 2, p. 27–122.

King, J. E. and T. S. Hida.
1954. Variations in zooplankton abundance in Hawaiian waters, 1950–52. U.S. Fish and Wildlife Service, Special Scientific Report—Fisheries No. 118. 66 p.
1957. Zooplankton abundance in Hawaiian waters, 1953–54. U.S. Fish and Wildlife Service, Special Scientific Report—Fisheries No. 221. 23 p.

Leipper, D. F. and E. R. Anderson.
1950. Sea temperatures, Hawaiian Island area. Pacific Science, vol. IV, No. 3, p. 228–248.

LIST, R. J.
1951. Smithsonian Meteorological Tables, 6th revised edition. Smithsonian Miscellaneous Collections, vol. 114. Smithsonian Institution Washington. 527 p.

LUMBY, J. R.
1956. The depth of the wind-produced homogeneous layer in the oceans. Great Britain, Minister of Agriculture, Fisheries and Food, Fish. Investigations Ser. 2, vol. 20, No. 2, p. 1–12.

McDONALD, W. F.
1938. Atlas of climatic charts of the oceans. U.S. Weather Bureau, Washington.

McGARY, J. W.
1955. Mid-Pacific oceanography, Part VI, Hawaiian offshore waters, December 1949–November 1951. U.S. Fish and Wildlife Service, Special Scientific Report—Fisheries No. 152. 138 p.

McGARY, J. W. and E. D. STROUP.
1956. Mid-Pacific oceanography, Part VIII, middle latitude waters, January–March 1954. U.S. Fish and Wildlife Service, Special Scientific Report—Fisheries No. 180. 173 p.

MUNK, W. H. and E. R. ANDERSON.
1948. Notes on a theory of the thermocline. Journal of Marine Research, vol. VII, No. 3, p. 276–303.

NATIONAL DEFENSE RESEARCH COMMITTEE, OFFICE OF SCIENTIFIC RESEARCH AND DEVELOPMENT.
1946. Application of oceanography to subsurface warfare. Reprinted 1951. National Research Council and Office of Naval Research. Washington. 106 p.

OCEANOGRAPHIC OBSERVATIONS OF THE PACIFIC: 1955
1960. THE NORPAC Data Volume. University of California Press, Berkeley. 582 p.

RIEHL, H., T. C. YEH, J. S. MALKUS, AND N. E. LA SEUR
1951. The northeast trade of the Pacific Ocean. Quarterly Journal of the Royal Meteorological Society, vol. 77, No. 334, p. 598–626.

ROBINSON, MARGARET K.
1954. Sea temperature in the Marshall Islands area. Bikini and nearby atolls. Part 2, Oceanography (physical). Geological Survey Professional Paper 260–B,C,D.

SCHOTT, G.
1935. Geographie des Indischen und Stillen Ozeans. C. Boysen, Hamburg. 413 p.

SECKEL, G. R.
1955. Mid-Pacific oceanography, Part VII, Hawaiian offshore waters, September 1952–August 1953. U.S. Fish and Wildlife Service, Special Scientific Report—Fisheries No. 164. 250 p.

STROUP, E. D.
1954. Mid-Pacific oceanography. Part IV. Transequatorial waters, January–March 1952. U.S. Fish and Wildlife Service, Special Scientific Report—Fisheries No. 135. 52 p.

SVERDRUP, H. V.
1936. Das maritime Verdunstungs problem. Annalen der Hydrographie und maritimen Meteorologie, vol. 64, p. 41–47.

SVERDRUP, H. V., M. W. JOHNSON AND R. H. FLEMING.
1942. The oceans; their physics, chemistry and general biology. Prentice-Hall, New York. 1087 p.

U.S. NAVY, CHIEF OF NAVAL OPERATIONS.
1956. U.S. Navy marine climatic atlas of the world. Vol. II. North Pacific Ocean. 275 p.

WALDRON, K., E. L. NAKAMURA, AND H. H. SHIPPEN.
Changes in the catch of skipjack and in their environment, Hawaiian waters, 1955–56. U.S. Bureau of Commercial Fisheries Biological Laboratory, Honolulu. (Manuscript.)

YAMASHITA, D. T.
1958. Analysis of catch statistics of the Hawaiian skipjack fishery. U.S. Fish and Wildlife Service, Fishery Bulletin, No. 134, vol. 58, p. 253–278.

APPENDIX A

SOURCE OF DATA

The data used in the Atlas were primarily collected during the years from World War II to 1957 in the area bounded by 10° N., 30° N., 150° W. and 180°.

The surface temperatures and depths of mixed layer were obtained from the bathythermograph deck at the Scripps Institution of Oceanography through the kind cooperation of Mrs. Margaret Robinson. The deck contained between 10,000 and 11,000 cards from bathythermograph observations made through 1955 by the staff of the Biological Laboratory, U.S. Bureau of Commercial Fisheries (Honolulu), the Scripps Institution of Oceanography, the U.S. Coast Guard, and the U.S. Navy. These data were supplemented by additional observations of the Honolulu Biological Laboratory through 1957.

Surface salinities were obtained from published oceanographic cruise reports, supplemented by unpublished data from the files of the Honolulu Biological Laboratory.

The dynamic topography, chart IV, was drawn from published data by Austin (1954, 1957), Bruneau et al. (1953), Cromwell (1951), Cromwell and Austin (1954), Fleming et al. (1945), Holtsmark (1949), McGary (1955), McGary and Stroup (1956), Oceanographic Observations of the Pacific: 1955 (1960), Seckel (1955), and Stroup (1954). In addition, there were some unpublished data from the files of the Scripps Institution of Oceanography which are scheduled for publication in Oceanic Observations of the Pacific.

TREATMENT OF DATA

Charts I and II, the distribution of the depth of the mixed layer and the surface temperature were all based on bathythermograph observations which were read and tabulated by 1° squares. These data were then averaged for each month of each year. Since in the Hawaiian region meridional gradients are generally greater than zonal gradients, the averaged data were plotted for each month in the ten meridional strips: 150° to 152° W., 153° to 155° W., 156° to 158° W., 159° to 161° W., 162° to 164° W., 165° to 167° W., 168° to 170° W., 171° to 173° W., 174° to 176° W., and 177° to 179° W. Needless to say, data for various months in different areas were missing or biased toward a single year. These difficulties were in part overcome by interpolation from seasonal curves and from comparisons with adjacent meridional distribution. The meridional surface temperature and depth of mixed layer profiles were then used to draw the monthly charts, where smoothing was done only after re-examination of the data.

Scarcity of salinity and dynamic height data prevented construction of monthly or quarterly charts. In grouping the data for the construction of two charts, a compromise between months of maximum observations and months of oceanographic significance had to be made. By "grouping data" is meant plotting all the observations for a period of months onto a single chart and then drawing contours through the mean values.

The number of salinity observations were relatively high during June to September and during January to March and predominated in the eastern portion of the region. On the basis of the seasonal salinity variation, the April to August data and the November to February data were grouped to draw chart III, representing the low and high salinity period near Hawaii, respectively. This grouping of months does not quite correspond with the maximum occurrence of data, nor, as is apparent from the salinity discussion in Part I, is it in phase with the high or low salinity north of 15° N. generally, or the extremes in the southeast portion of the region.

Significant grouping of the dynamic height data, which were collected predominantly during June to August and January to March, was more difficult. In the estimation of geostrophic currents, gradients rather than the absolute magnitudes of geopotentials are of importance. This makes grouping of several months' data, collected during a number of years, questionable. In addition, the dynamically significant periods as reflected in the geopotential topography are not known and may not correspond with any or all of the advective periods discussed in the atlas. Despite these shortcomings, the data from December to April and June to October were grouped to draw chart IV. These, therefore, roughly bracket the period of low advection during the winter and high advection during the summer months.

APPENDIX B

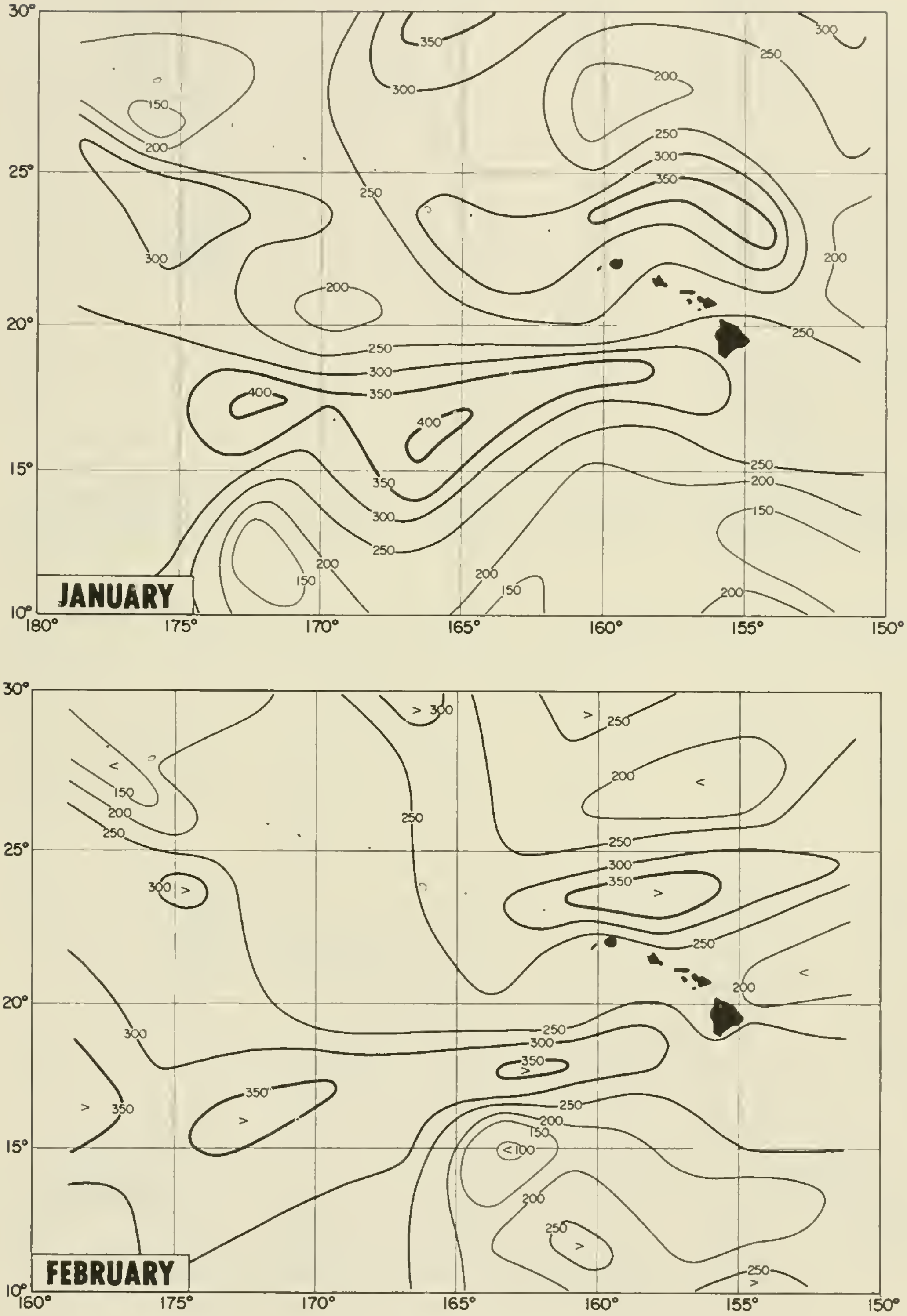


Chart I.—Distribution of the depth of mixed layer feet.

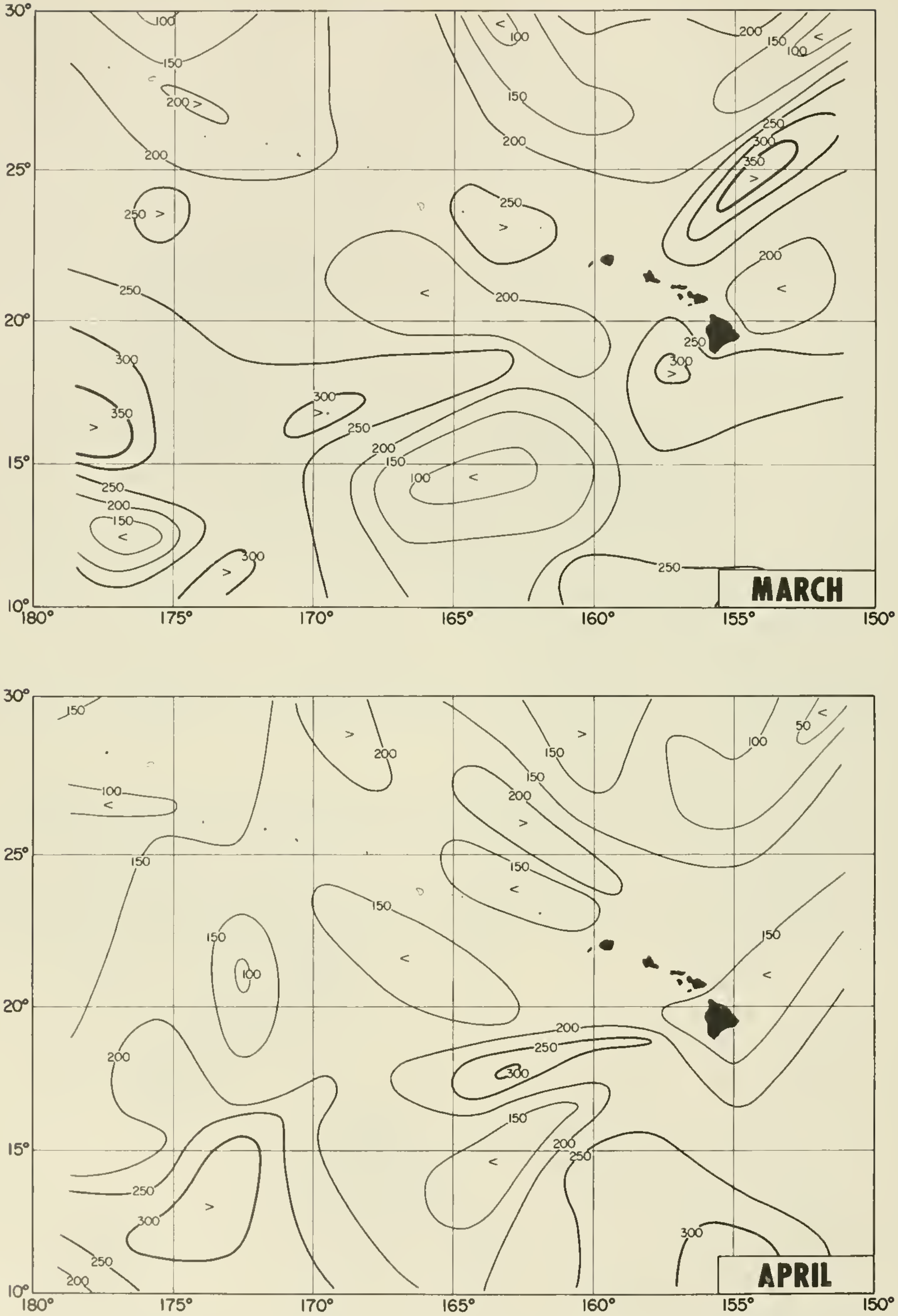


Chart I.—Distribution of depth of mixed layer (feet)—Continued.

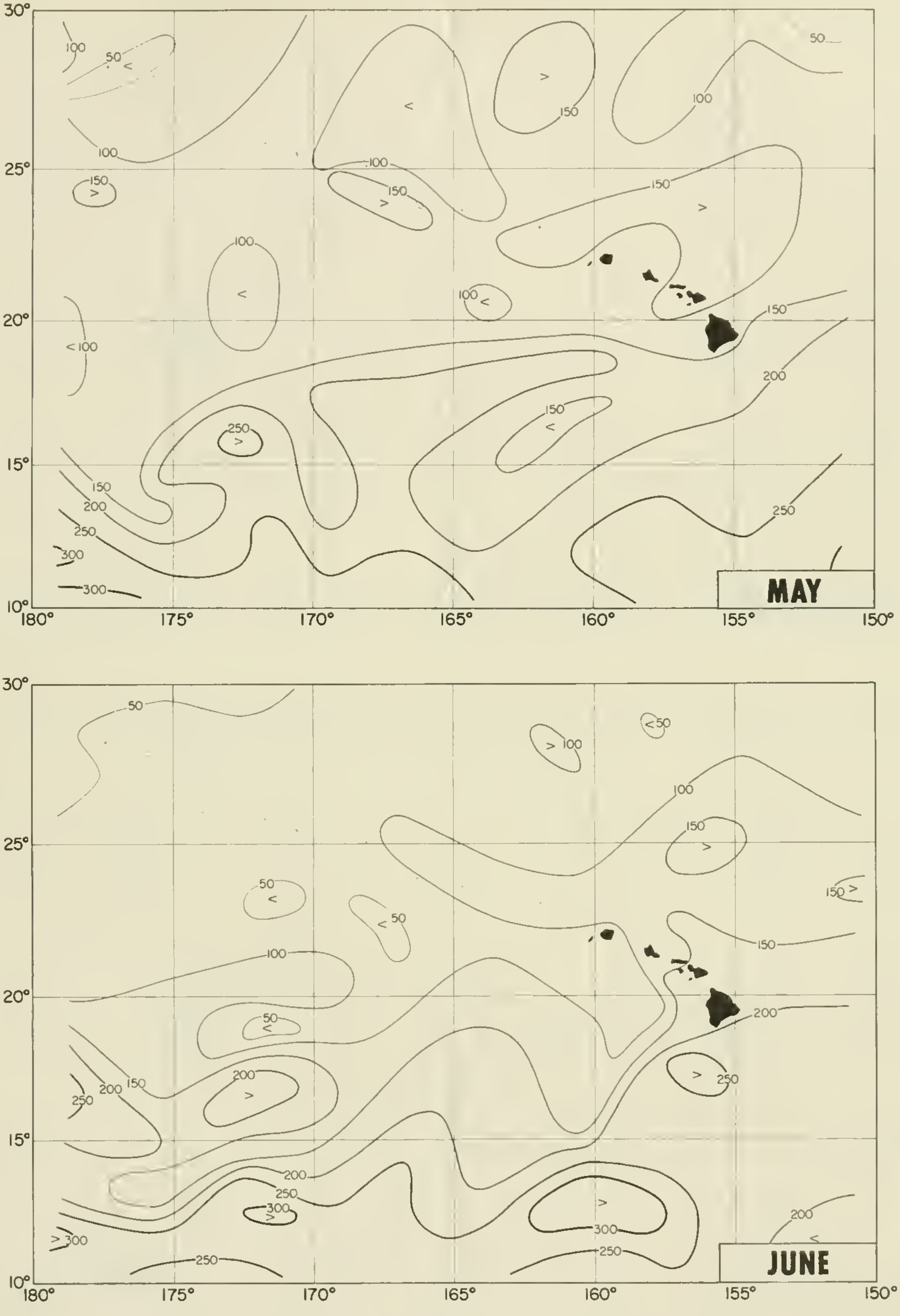


Chart I.—Distribution of depth of mixed layer (feet)—Continued.

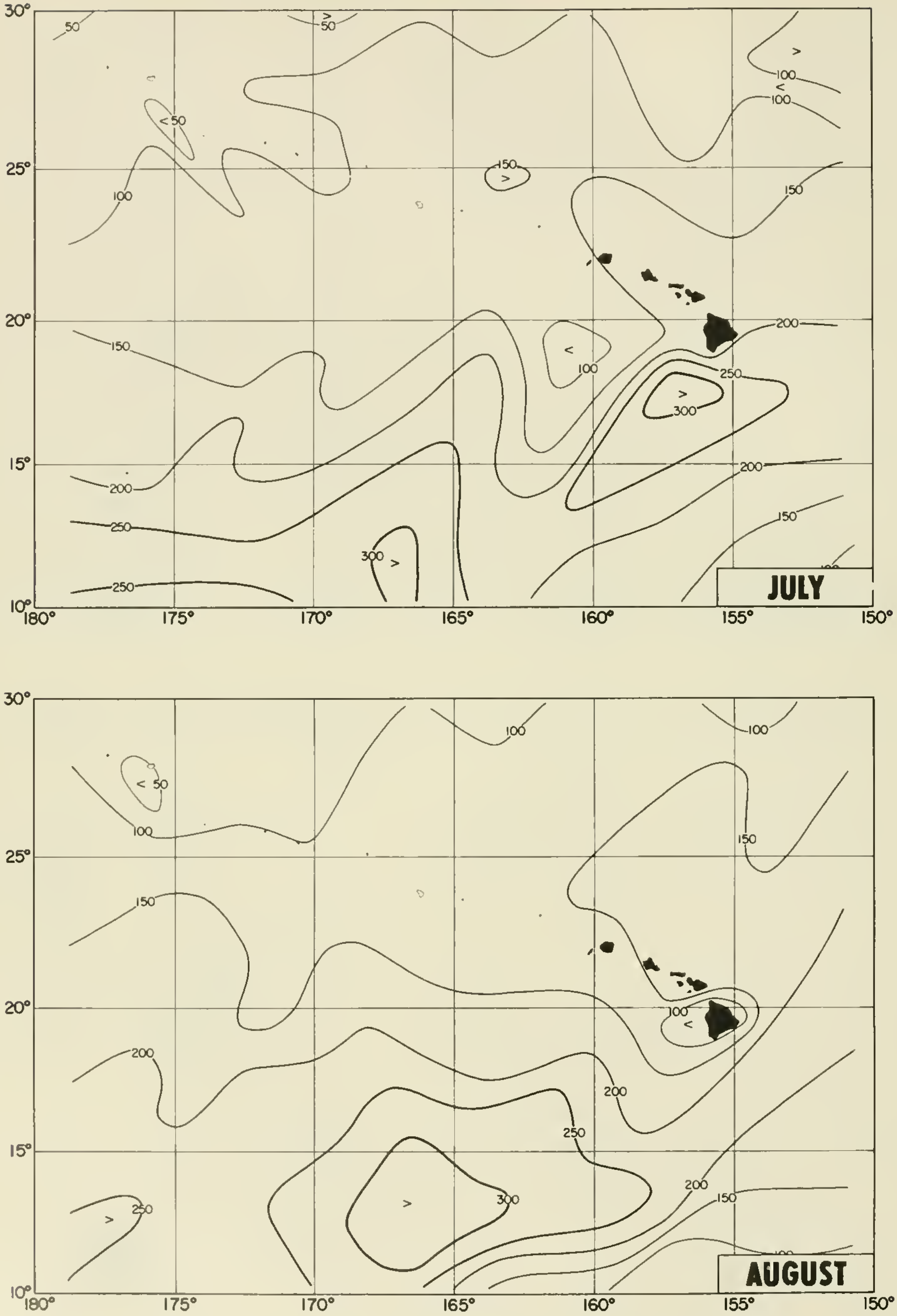


Chart I.—Distribution of depth of mixed layer (feet)—Continued.

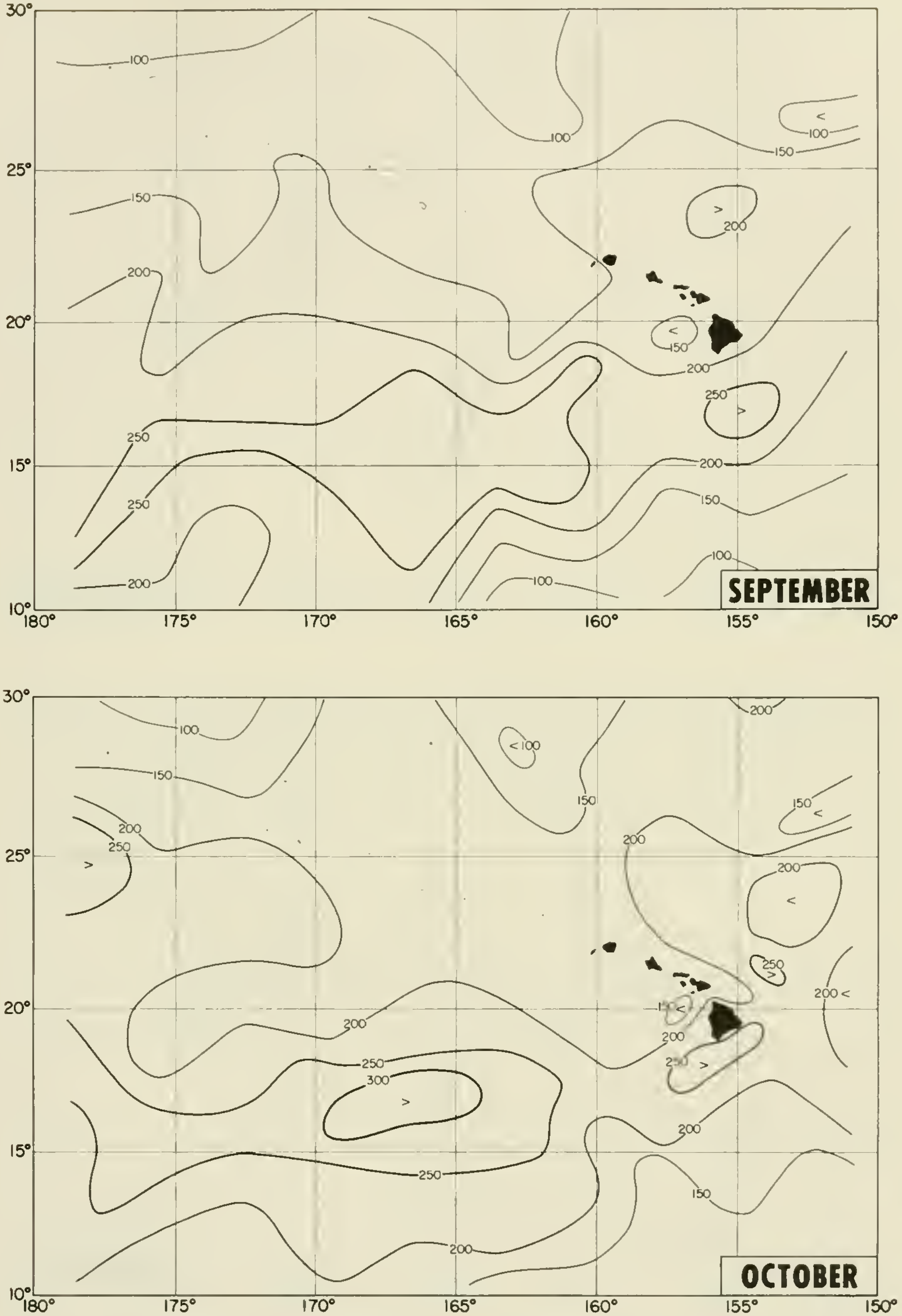


Chart I.—Distribution of depth of mixed layer (feet)—Continued.

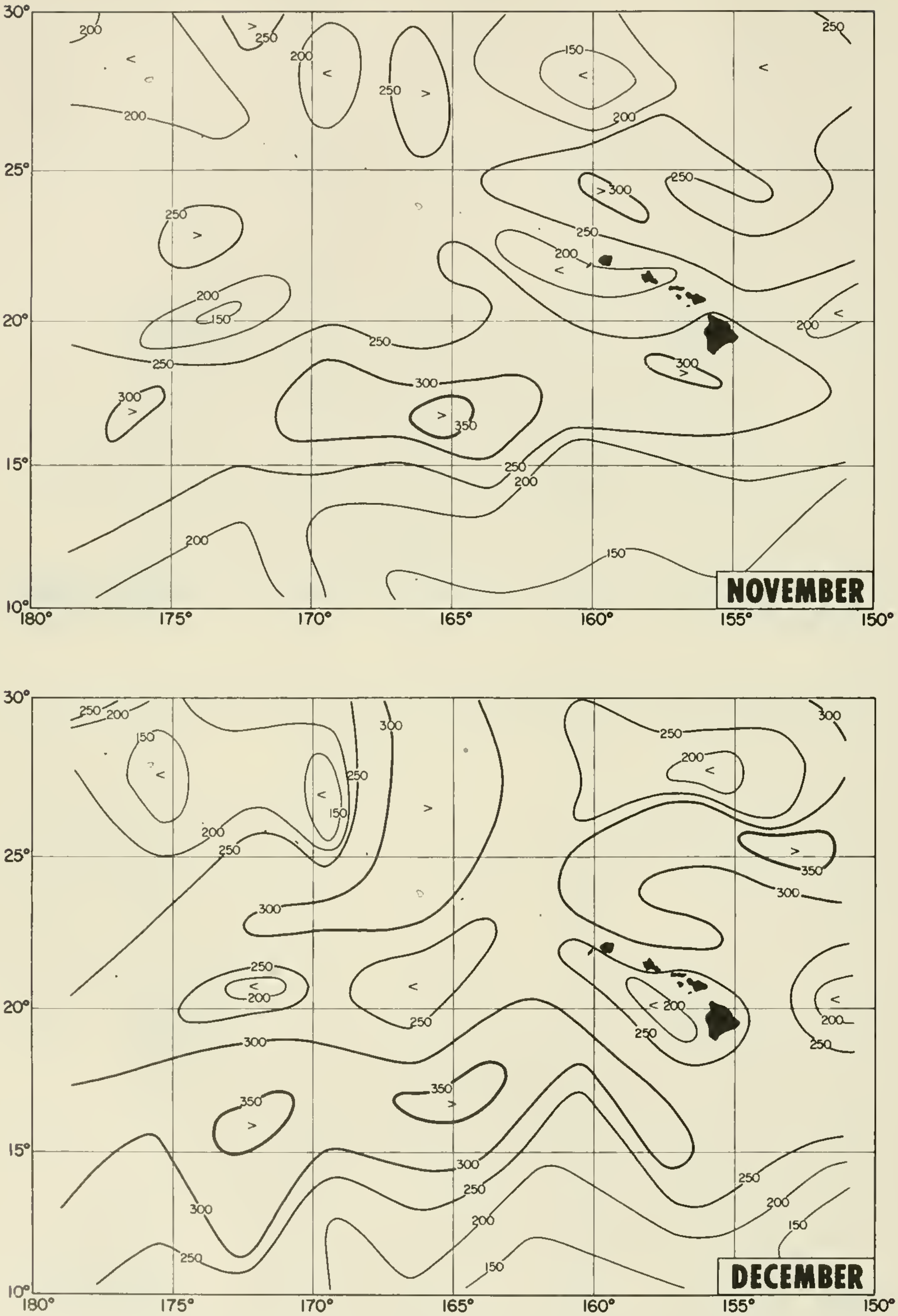


Chart I.—Distribution of depth of mixed layer (feet)—Continued.

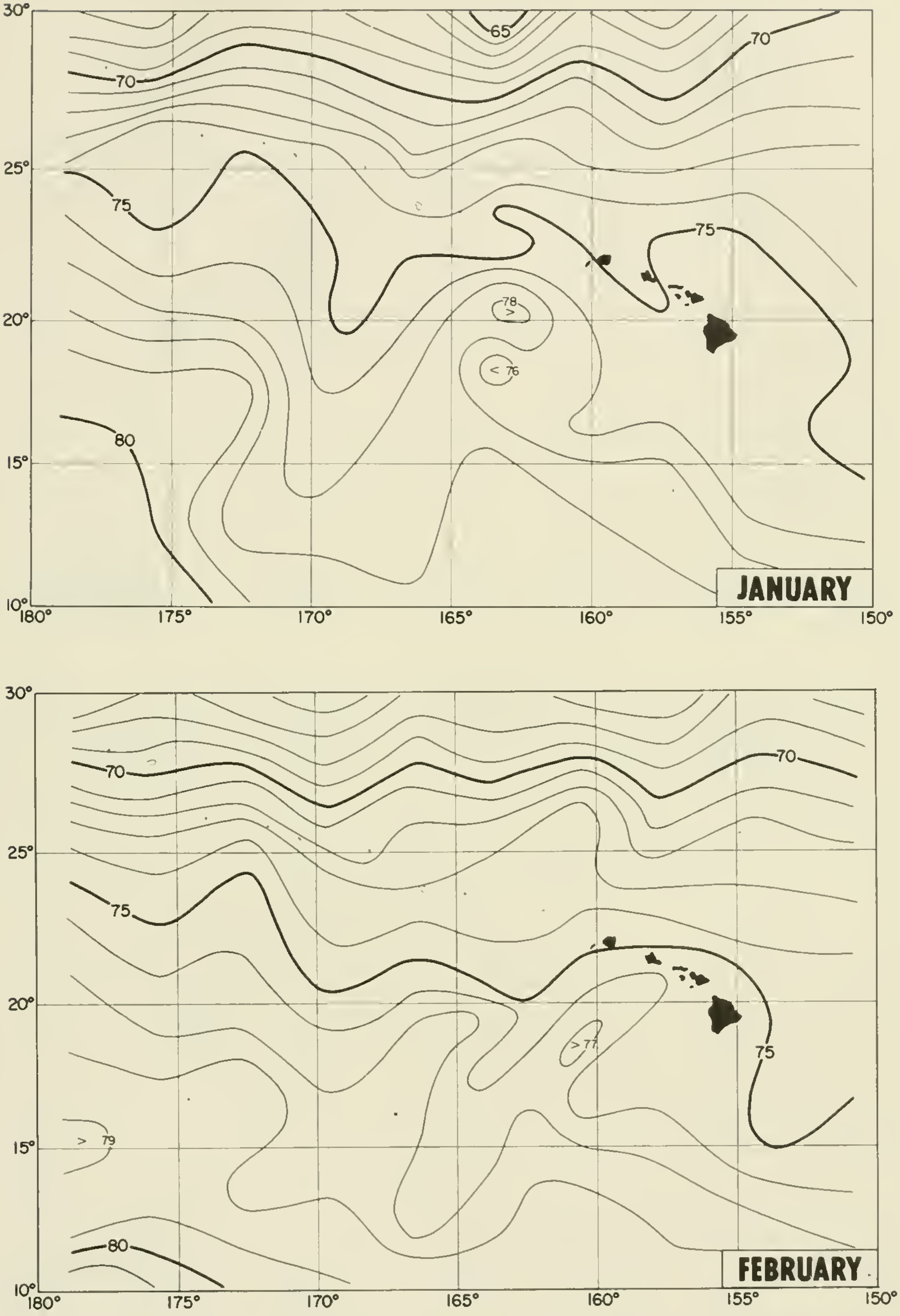
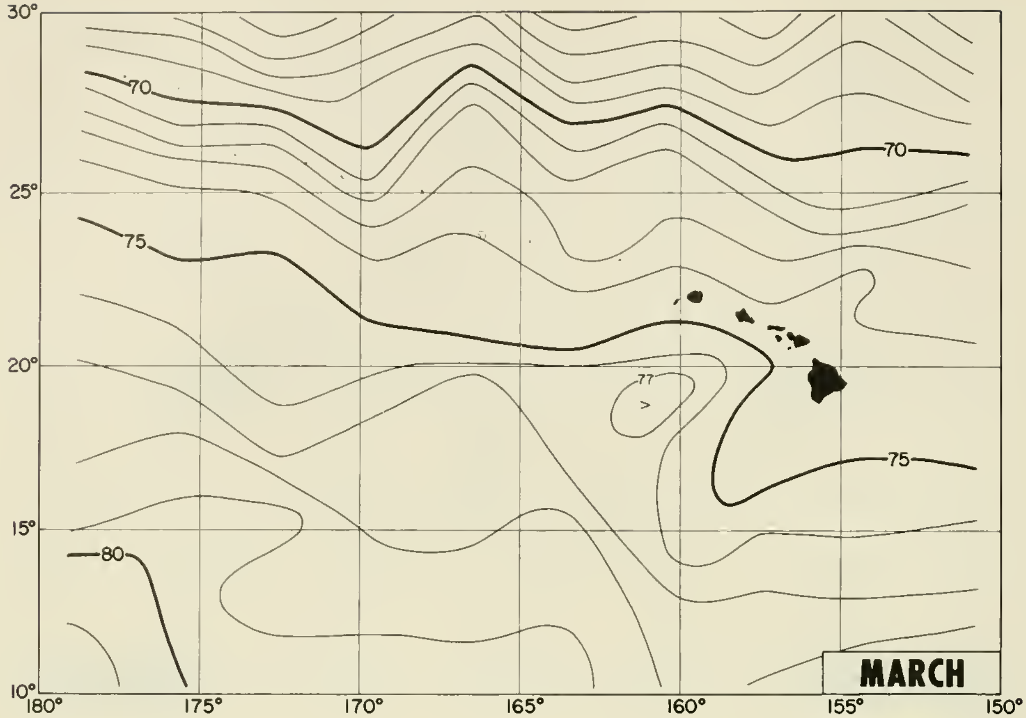


Chart II.—Distribution of surface temperature (° F.)



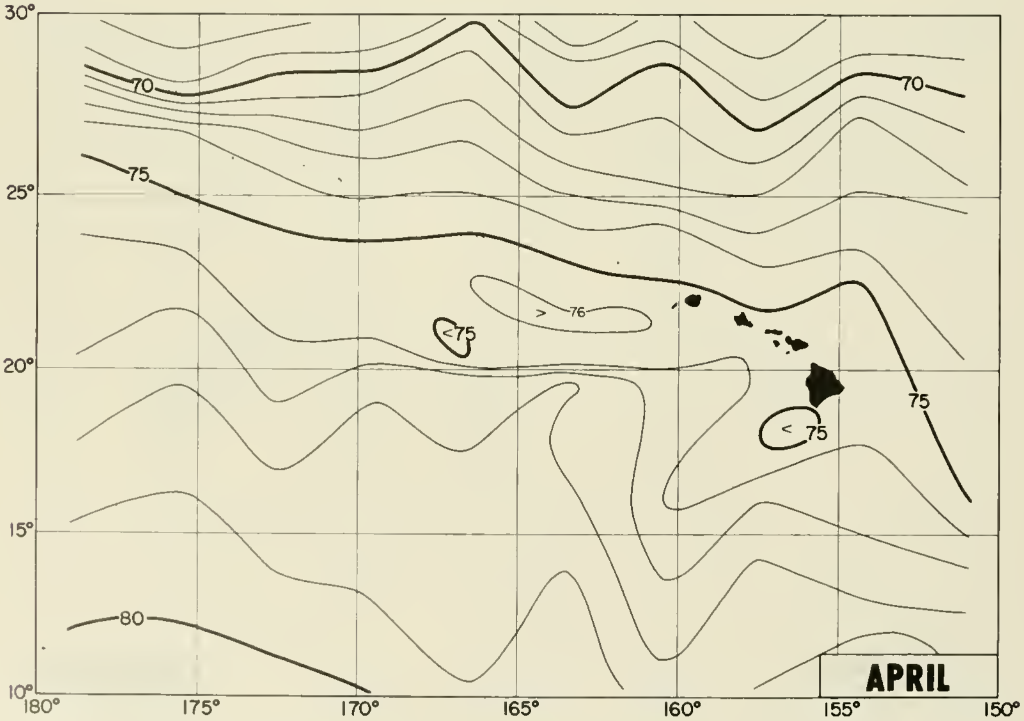


Chart II.—Distribution of surface temperature (° F.)—Continued.

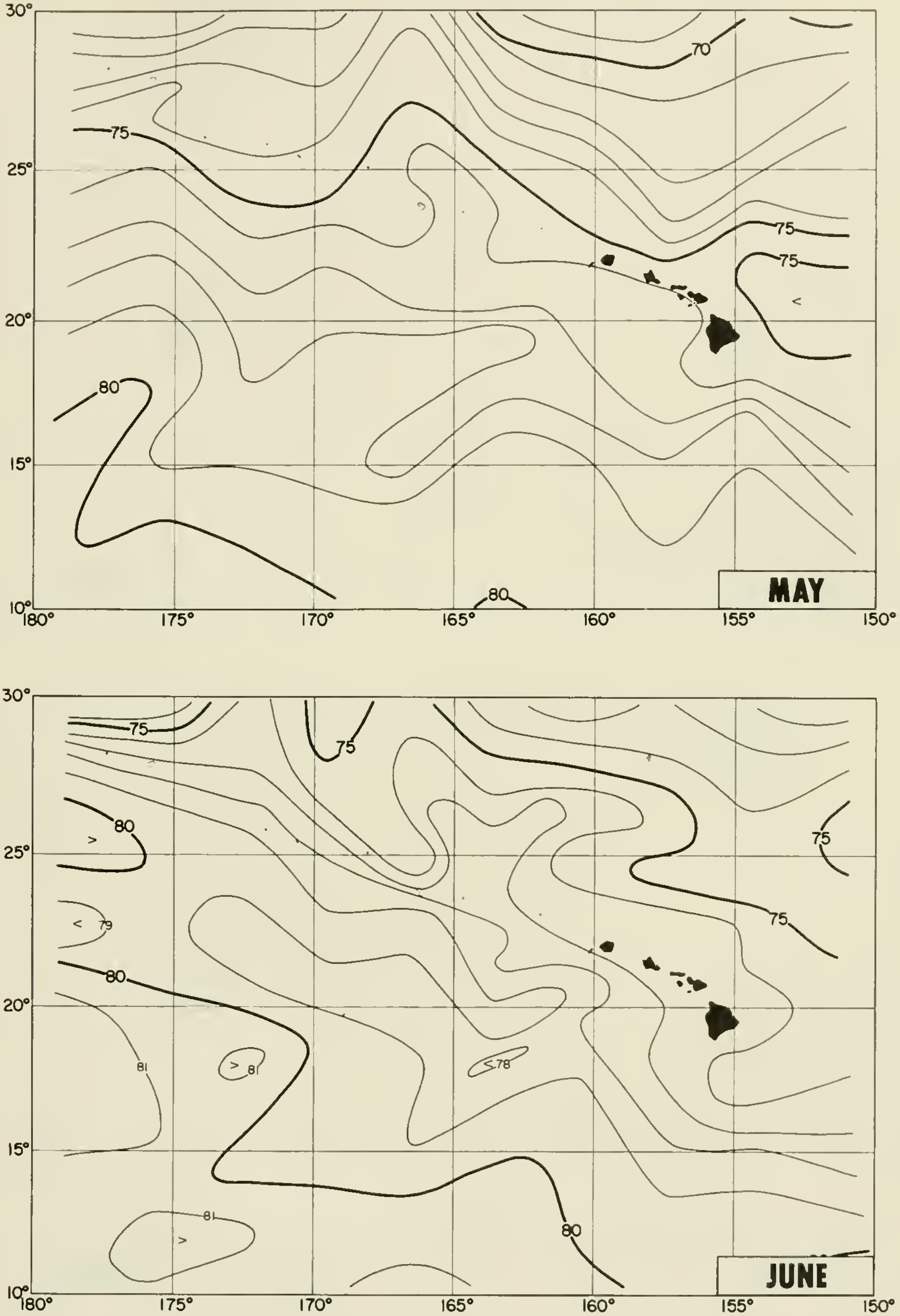


CHART II.—Distribution of surface temperature (° F.)—Continued.

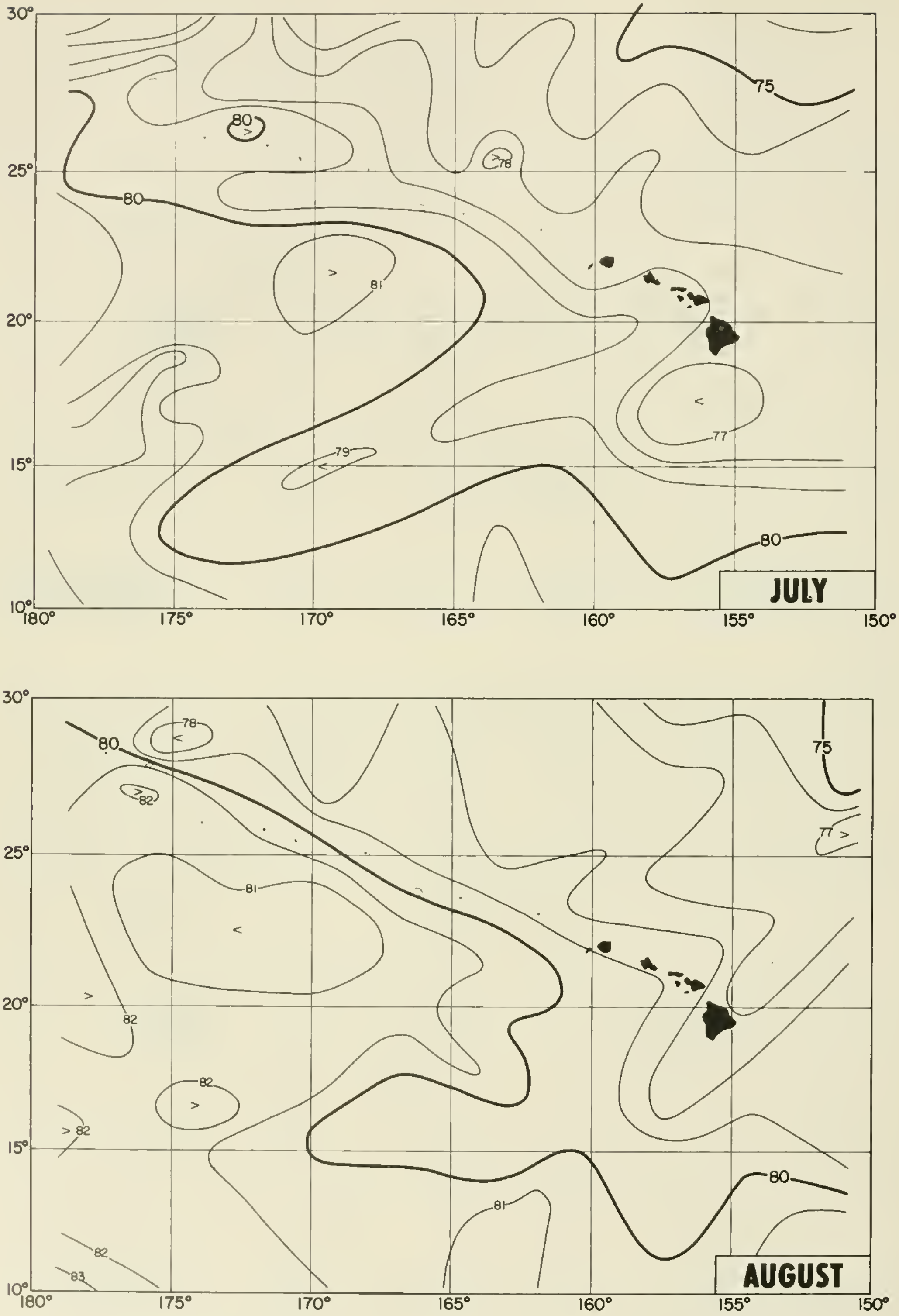


Chart II.—Distribution of surface temperature (° F.)—Continued.

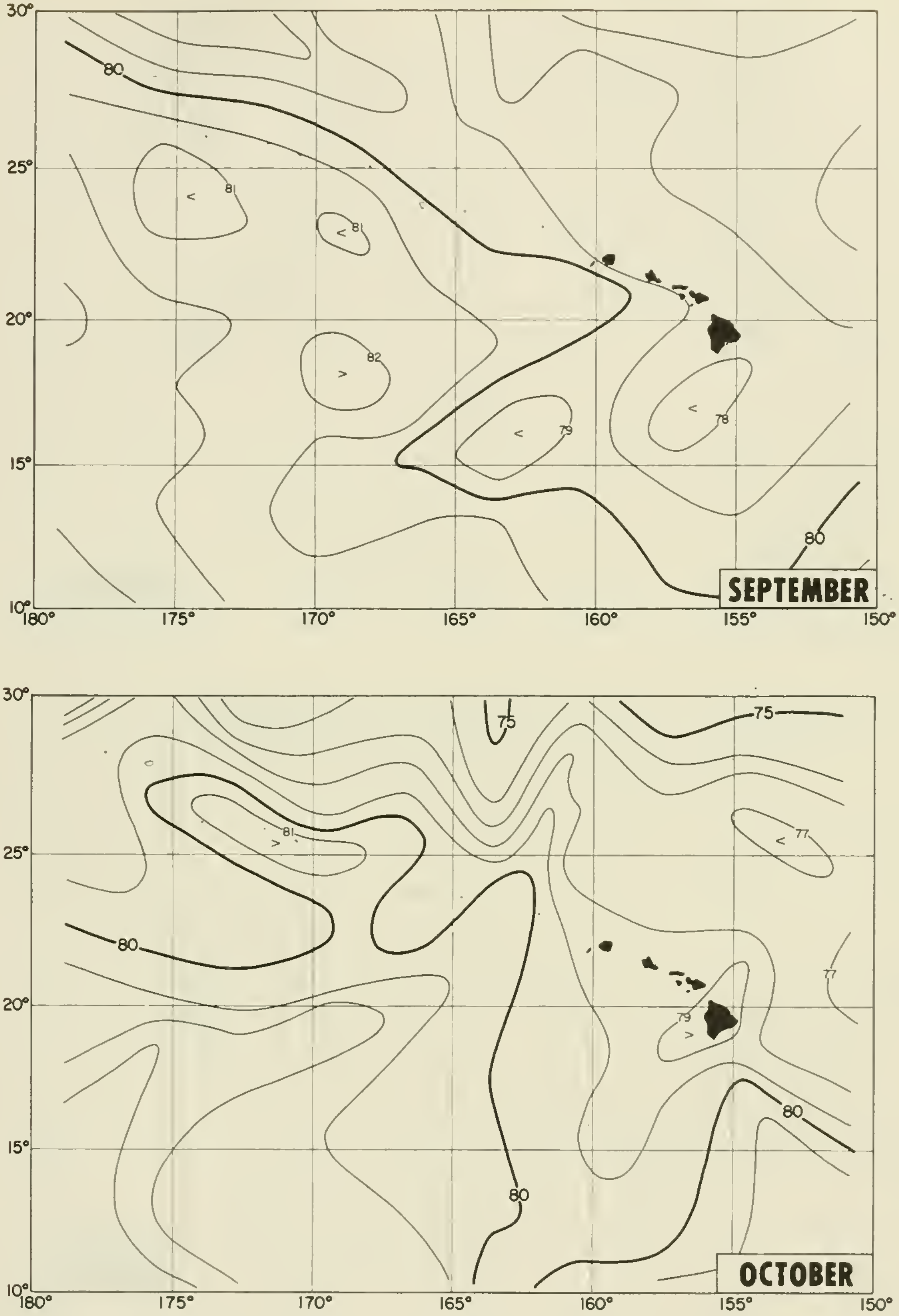


Chart II.—Distribution of surface temperature (° F.)—Continued.

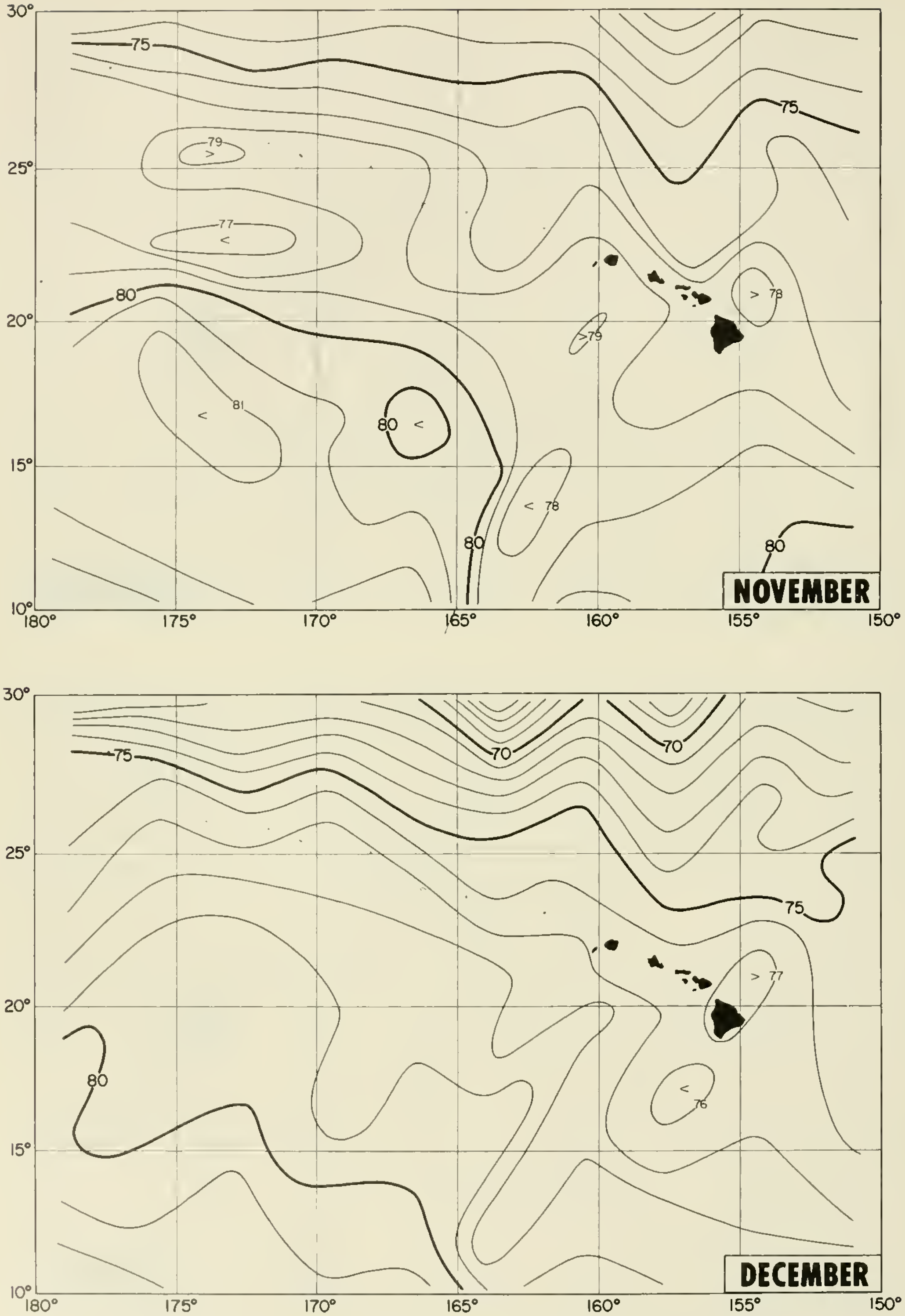


CHART II.—Distribution of surface temperature (° F.)—Continued.

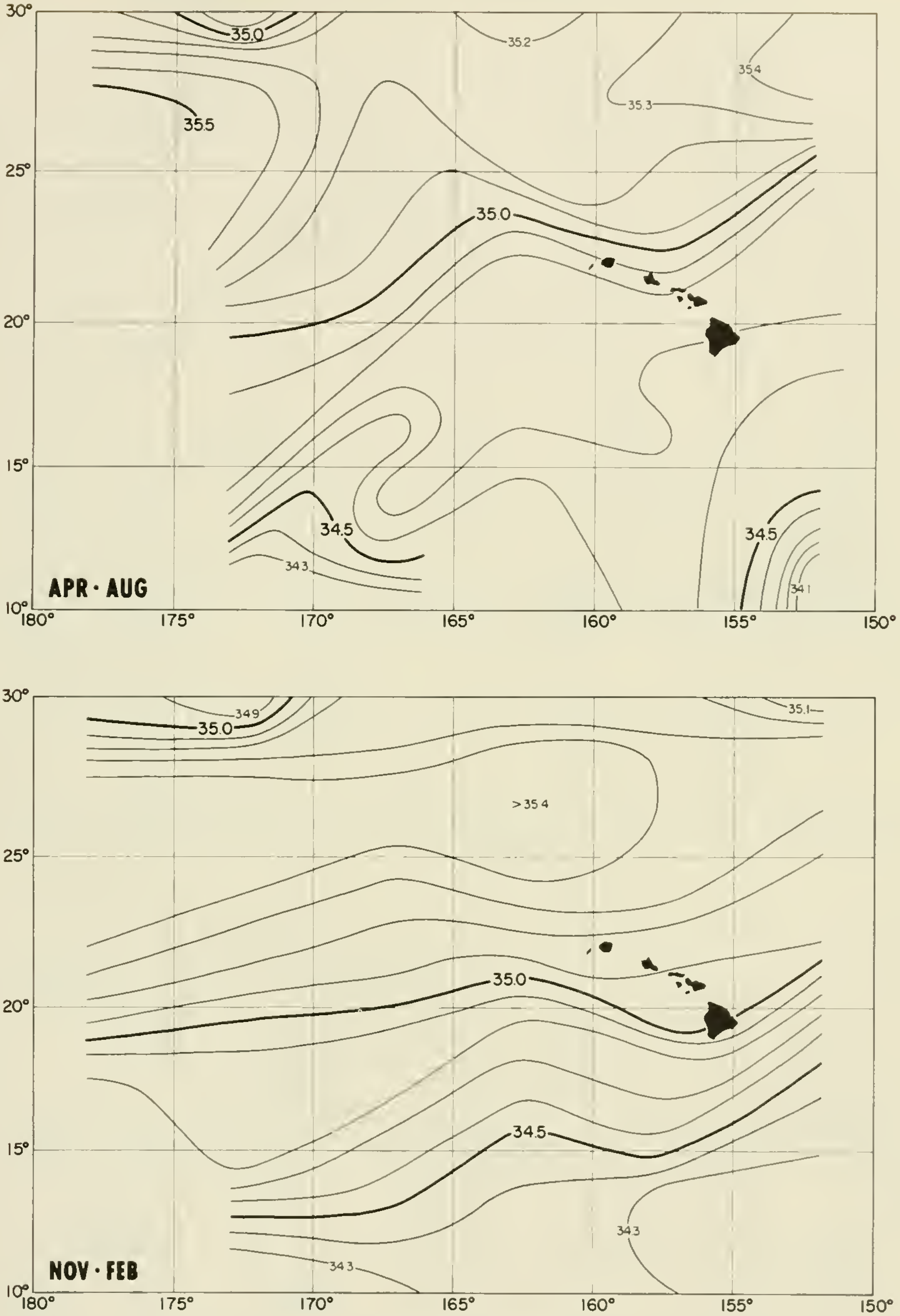


Chart III.—Distribution of surface salinity (parts per thousand).

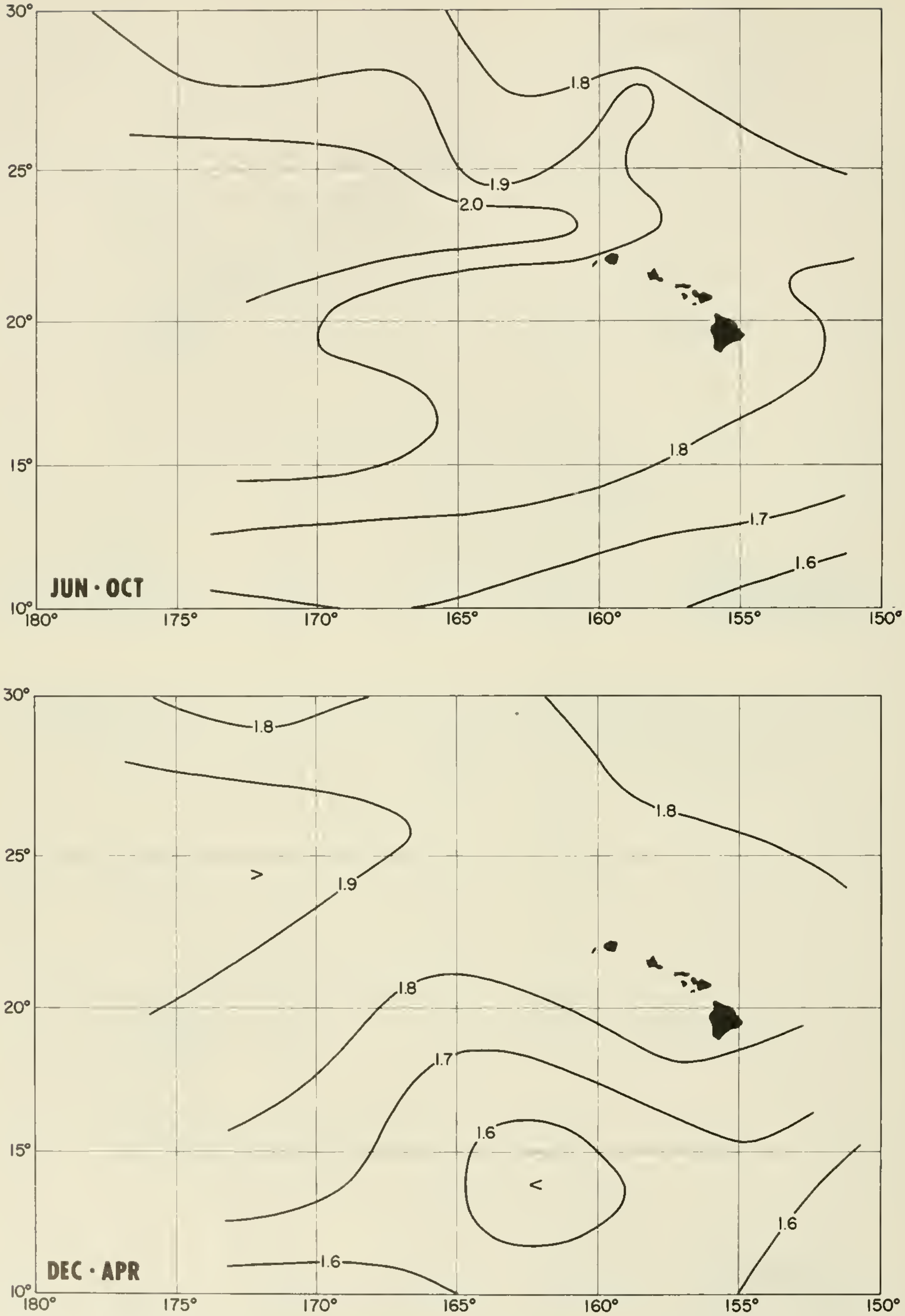


CHART IV.—The surface dynamic topography (in dynamic meters relative to 1,000 M.).

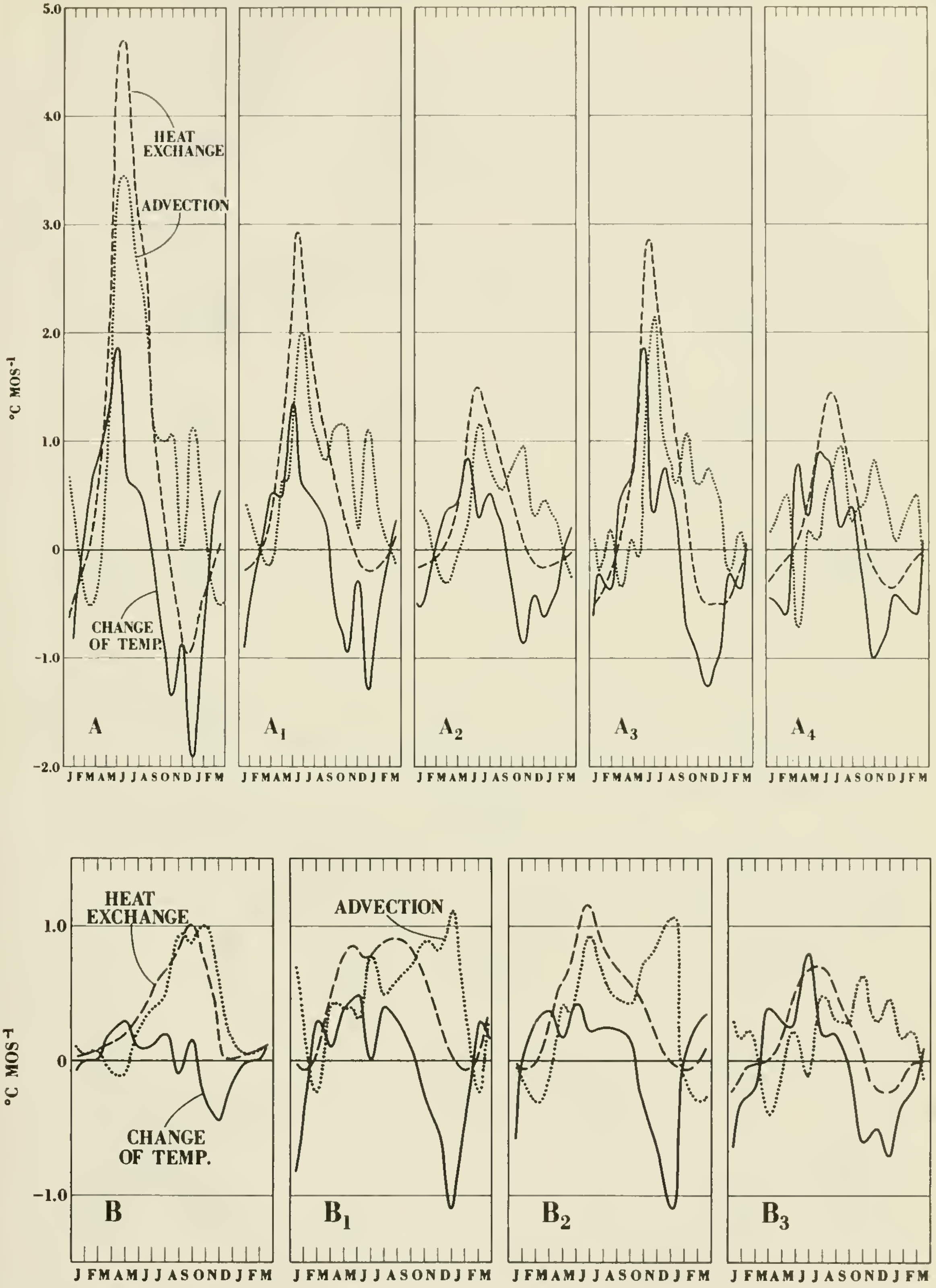


Chart V.—Characteristic asvection diagrams. For the areas designated by A, A$_1$, and so forth, see figure 24, page 397.

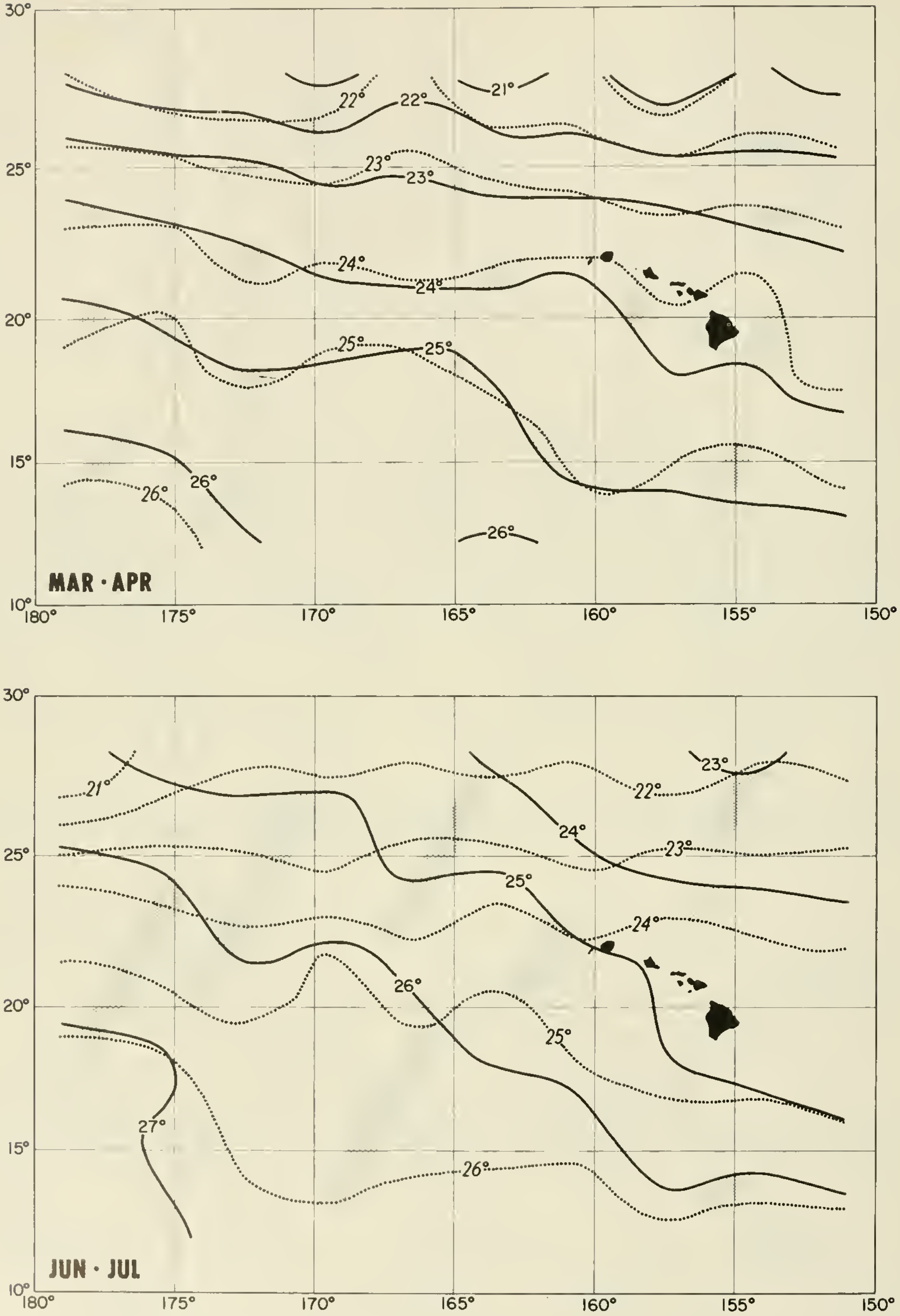


Chart VI.—Heat advection chart (° C.)

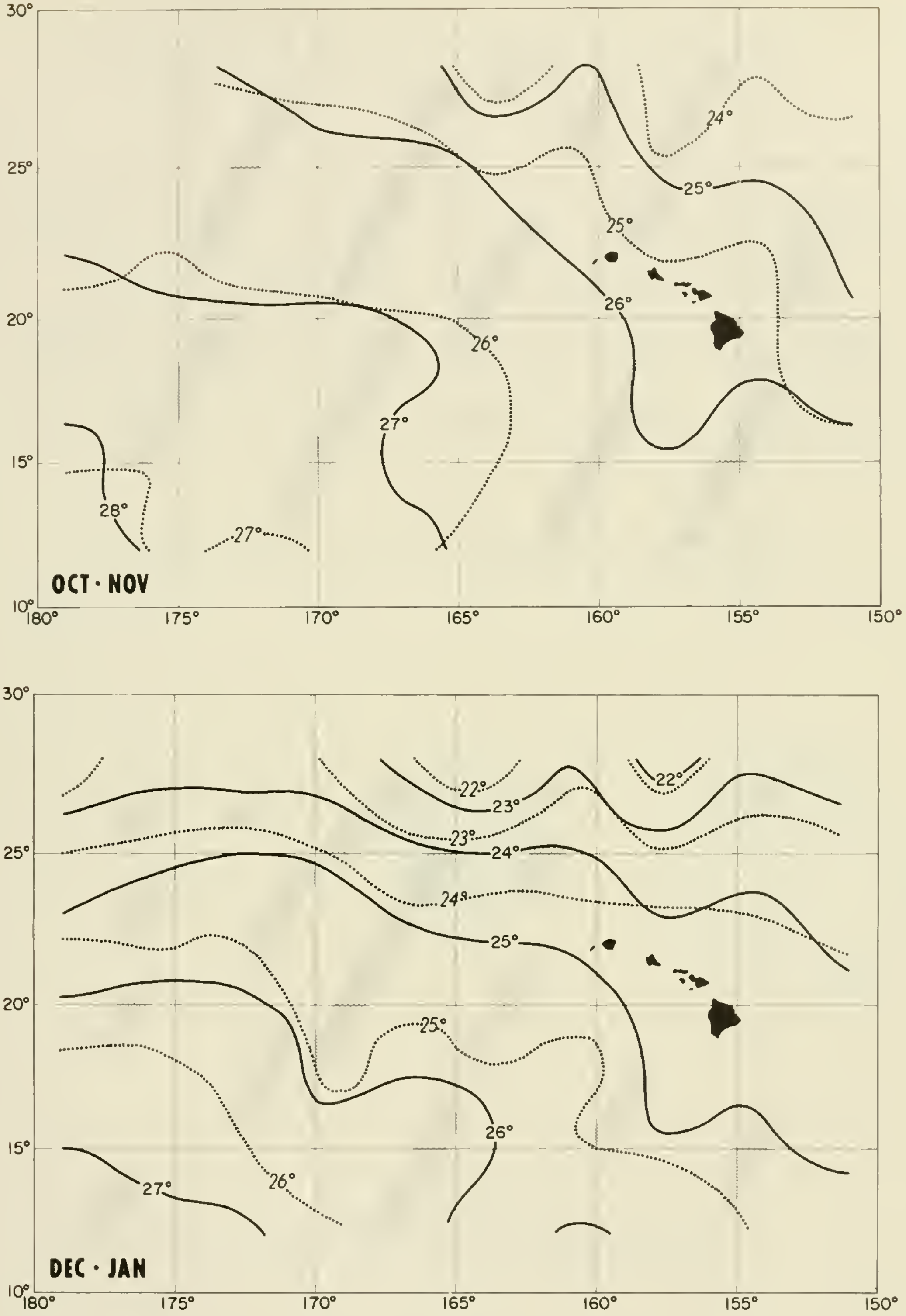


Chart VI.—Heat advection charts (° C.)—Continued.

UNITED STATES DEPARTMENT OF THE INTERIOR, Stewart L. Udall, *Secretary*

FISH AND WILDLIFE SERVICE, Clarence L. Pautzke, *Commissioner*

BUREAU OF COMMERCIAL FISHERIES, Donald L. McKernan, *Director*

INFLUENCE OF EARLY MATURING FEMALES ON REPRODUCTIVE POTENTIAL OF COLUMBIA RIVER BLUEBACK SALMON (*Oncorhynchus nerka*)

By RICHARD L. MAJOR and DONOVAN R. CRADDOCK

March 3, 1849

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ABSTRACT

Early maturing fish that have spent only one year in the ocean are common in the spawning escapements of Columbia River blueback salmon (*Oncorhynchus nerka*), particularly in the Okanogan tributary. The unusually high incidence of these 1-year-ocean fish in 1953, however, led to a study to determine the average fecundity of the ocean-age groups composing the runs, and to assess the effect of varying age and sex composition on estimates of reproductive potential.

A fecundity study in 1957–59 revealed that the average egg content of 1-year-ocean females was approximately one-third less than that of 2-year-ocean females. The average egg content of 3-year-ocean females was, in turn, about one-fourth greater than that of 2-year-ocean females.

Analysis of the age group fecundity and sex ratio data showed that the number of spawners or even female spawners does not always accurately portray the reproductive potential of an escapement. Erroneous reproduction estimates seriously distort escapement-return relationships.

INFLUENCE OF EARLY MATURING FEMALES ON REPRODUCTIVE POTENTIAL OF COLUMBIA RIVER BLUEBACK SALMON (*Oncorhynchus nerka*)

By Richard L. Major and Donovan R. Craddock

Fishery Research Biologists, Bureau of Commercial Fisheries

Isolating the causes of variability in escapement-return relationships is among the most urgent problems in the biology and management of the Pacific salmons (*Oncorhynchus* spp.). Of primary concern are the causes of low numbers of fish in the returns. The fresh-water environment is widely thought to be more important than the marine environment in contributing to these subnormal returns.

Age and sex composition of the parent escapement are among the factors of recognized importance. For example, an escapement of normal size, but one containing females that are relatively few in number or small in size (young-ocean-age) will bring to the spawning ground a subnormal number of eggs. Hence, with all other factors affecting the return being similar, this escapement would produce a smaller return than would an escapement of fish normal in size, age, and sex composition.

Salmon runs to many Pacific coast streams contain small fish commonly called "jacks," that have matured after an ocean life shorter than normal for the species and the area. The occurrence of these precocious fish in the runs of Columbia River blueback salmon (*Oncorhynchus nerka*), known also as sockeye or red salmon, is unusual in three respects. First, they are relatively more abundant here than in most other systems, a feature compounded in the escapement because the gill net fishery below Bonneville Dam (fig. 1) is selective for larger fish. Second, they spawn mostly in a single tributary, the Okanogan River, although we occasionally observe individuals in the Wenatchee River system, the other major blueback spawning area in the Columbia River watershed. Finally, precocious blueback salmon (age 3_2's)[1] in the Okanogan River escapements contain a relatively high proportion of females.[1]

The high incidence of 1-year-ocean fish in the escapement of 1953 attracted wide attention. In that year, 52,182 small blueback were counted passing over Rock Island Dam on the main Columbia; this was 34 percent of the total count of 151,747 (table 1). Escapement to the Wenatchee River system reportedly contained few if any 3_2's in 1953.[2]

The Columbia River blueback runs include fish that mature at ages 3, 4, and 5 years. Although exact age-composition data are lacking, age 4 fish are known to dominate the runs. As a result, the relatively low return in 1957 revived interest in the 1953 escapement. Furthermore, examination of the escapement-return data (table 2) reveals that this cycle is one of only 2 out of 18 cycles observed, in which the return failed to exceed its parent escapement (1940 and 1953 escapements).

Efforts to explain low returns are ordinarily directed toward the isolation of one or more abnormal conditions which adversely affected production or survival of the progeny in fresh water. Among the factors of potential importance are: (1) unbalanced age and sex composition of the parent stock, (2) unfavorable environmental conditions during the early life history of the young fish and (3) mortalities connected with seaward migration.

Note.—Approved for publication May 12, 1961. Fishery Bulletin 191.

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[1] This method of designating the age of salmon, developed by Gilbert and Rich (1927), is described by Nelson (1959):

> A fish resulting from an egg laid in the spawning gravels in 1950 and that migrated to the ocean in 1952 and returned in 1955 is called a five-two and designated thus, 5_2. Such a fish would have emerged from the gravels of the spawning beds in the spring of 1951 and would have spent 1 growing season or summer in fresh water. In referring to its fresh-water history it is called a two-fresh-water fish, because it migrated seaward in its second year. It would have spent 3 full growing seasons, i.e., 1952, 1953, and 1954, and part of a fourth year in the ocean; but in referring to its ocean history it is called a three-ocean fish, because it returned as an adult in the third year following its seaward migration. A fish that migrated to the ocean in its third year and returned in its sixth is called a six-three and is designated 6_3.

[2] Personnel communication with Leonard A. Fulton, then project leader of the Columbia River blueback salmon studies, now with the U.S. Fish and Wildlife Service, Washington, D.C., and Alfred C. Gastineau, manager, Leavenworth National Fish Hatchery, Leavenworth, Wash.

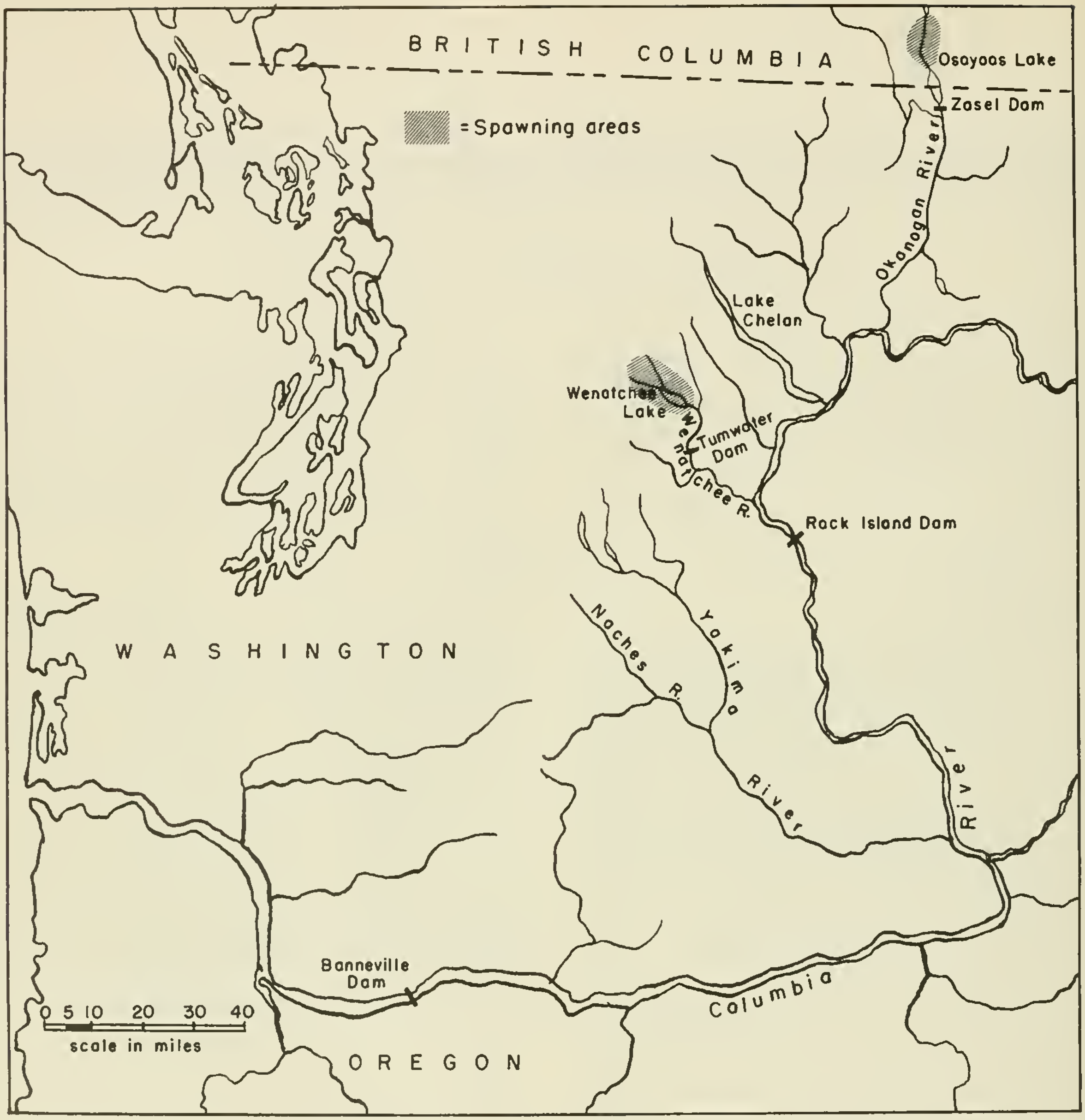

Figure 1.—The Columbia River and the major blueback salmon spawning areas and the locations of the dams important to this study.

TABLE 1.—*Incidence of small (3_2) blueback in the Columbia River since 1945* [1]

Year	Catch below Bonneville Dam	Bonneville Dam fishway count	Total run (catch below Bonneville Dam plus Bonneville Dam fishway count)	Rock Island Dam fishway count		
				Total	Small (3_2)	Percent small
1945	1,325	9,501	10,826	7,148	2,319	32
1946	25,601	74,376	99,977	44,970	6,457	14
1947	159,385	171,139	330,524	79,831	10,160	13
1948	11,647	131,541	143,188	84,184	4,912	6
1949	1,244	51,444	52,688	18,600	1,417	8
1950	33,576	77,993	111,569	50,134	11,258	22
1951	34,941	169,428	204,369	101,826	12,093	12
1952	135,717	184,645	320,362	114,349	9,478	8
1953	24,864	235,215	260,079	151,747	52,182	34
1954	48,474	130,107	178,581	91,234	14,486	16
1955	7,131	237,748	244,879	155,054	9,601	6
1956	45,822	156,418	202,240	92,443	17,880	19
1957	65,261	82,915	148,176	71,261	7,528	11
1958	190,325	122,389	312,714	98,716	18,233	18
1959	185,882	86,560	272,442	72,251	8,384	12

[1] *Sources of data:* Bonneville Dam fishway counts.—From Annual Fish Passage Report, North Pacific Division, Bonneville, The Dalles and McNary Dams, Columbia River, Oregon and Washington, 1958. U.S. Corps of Engineers, Portland and Walla Walla Districts. Also unpublished data, 1959. Catch below Bonneville Dam.—From Oregon Fish Commission, unpublished data. Rock Island Dam fishway counts.—From U.S. Fish and Wildlife Service, Bureau of Commercial Fisheries, Portland, Oreg.

TABLE 2.—*The escapement-return data for the Columbia River blueback runs for the brood years 1938–55*

Year (N)	Rock Island (year N) (all age groups)	Total run (Year N+4) (all age groups)	Escapement-return ratio
1938	17,095	94,238	5.51
1939	19,591	73,484	3.75
1940	27,093	24,565	0.91
1941	963	10,826	11.24
1942	16,340	99,977	6.11
1943	17,665	330,524	18.71
1944	5,035	143,188	28.43
1945	7,148	52,688	7.37
1946	45,030	111,569	2.47
1947	79,831	204,369	2.56
1948	84,627	320,362	3.78
1949	18,600	260,079	13.98
1950	50,134	178,581	3.56
1951	101,826	244,879	2.40
1952	114,349	202,240	1.76
1953	151,747	148,176	0.98
1954	91,234	312,714	3.43
1955	155,055	272,442	1.75

Because the lack of more complete data prohibits a comprehensive examination of the latter two items, we shall examine only the first alternative in this report. If age 3_2 females were highly abundant in the 1953 escapement and if these small females contain fewer eggs than normal age 4_2 females, then the egg potential of that escapement may have been much lower than the number of spawners or even female spawners would indicate.

Our main objectives are, therefore: (1) to estimate mean fecundity of the various age groups that spawn in the Okanogan River and (2) to assess the effect of age and sex composition on estimates of egg potential of the Okanogan River spawning escapements. In the light of our findings, we shall then examine and discuss other aspects of the early maturing fish.

The assistance of the Oregon Fish Commission aided this study materially. The authors are particularly indebted to Lawrence Korn for collecting the ovary samples in 1958.

METHODS AND MATERIALS

Collection and Preservation of Samples

Estimates of age group fecundity are from fish taken both in the tributary spawning streams and in the commercial catch below Bonneville Dam on the main Columbia River. In 1957 the racial sampling program of the International North Pacific Fisheries Commission made available to us 34 females taken at Tumwater Dam on the Wenatchee River and 23 captured at Zosel Dam on the Okanogan River. Samples from this source were not available in 1958; thus we had to find samples elsewhere, preferably from the commercial catch to avoid killing potential spawners in the tributaries. In 1958 sixty-two fish were selected from the commercial catch to represent the length-range of female blueback. Similar sampling provided 27 fish in 1959. Owing to a scarcity of small fish in the catch, the 1959 catch sample was augmented with 10 small fish taken from the fishway at Rock Island Dam.

Members of the 4_2 age group from both the Okanogan and Wenatchee areas are mixed in the catch, and we have no method of classifying catch samples into area of origin. Consequently, it is necessary to assume that fecundity estimates derived from this source accurately represent the Okanogan River spawning population. A statistical test to support this assumption is presented in a later section.

From each fish the fork length was recorded and a scale sample taken for age determination. Ovaries were removed, wrapped in cheesecloth, labeled, and preserved in 10-percent formalin. Total, fresh-water and ocean ages were determined by the age analysis unit at the Bureau of Commercial Fisheries Seattle Biological Laboratory.

Egg Enumeration

Estimation of total egg content for each fish proceeded as follows: Each pair of ovaries was washed of excess formalin, drained of excess moisture, freed of tissue, then weighed to the nearest hundredth gram. Eggs were weighed and enumerated from cross-sectional samples from each ovary combined to approximate 10 percent of the total egg weight. Total egg count was then computed on a proportional weight-count basis, with the assumption that the sample was representative of the entire ovary.

Spawning Ground Surveys

Spawning grounds of the Okanogan River have been surveyed each year since 1947, except 1950. Gangmark and Fulton (1952) describe the method used to estimate the size of spawning populations.

Estimates of age and sex composition, computed for the years 1953 and 1956 through 1959, are based on standardized collections of fresh dead fish, which were picked up in proportion to their availability at intervals throughout the entire period when spawners are dying.

The sampling methods described herein are not rigorous from a statistical viewpoint. Yet we believe them to be adequate for purposes of this report, which represents the difficult transition from the qualitative to quantitative stages of investigation. Under appropriate headings of the next section are discussed certain preliminary tests which are pertinent to the sampling and to the data thereby derived.

RESULTS

Age Group Fecundity

In the previous section we indicate that because the catch contains 4_2's from both the Wenatchee and Okanogan populations, we can merely assume that mean fecundity estimates derived from this source are representative of the Okanogan population. The assumption is supported by the following test:

We hypothesize that no fecundity difference exists between the 4_2's of the two river systems. Comparison of the 1957 sample-means of 16 Okanogan and 17 Wenatchee fish by t-test reveals no significant difference at the 5 percent level ($t=0.15$ with 15 d.f.). On the basis of this evidence the hypothesis is not rejected, and, with reasonable assurance that it holds, we assume that the fecundity difference is not large and that estimates derived from the catch will accurately represent either area.

To determine whether a bias exists in our method of estimating the mean egg content of individual fish, we used a t-test to compare the actual and estimated mean egg content of a randomly selected subsample of 21 fish (table 3). The average difference between the actual and estimated means is 40 eggs, the standard error of the mean, 27 eggs. Although it appears that we are overestimating, the difference is not significant at the 5 percent level ($t=1.49$ with 20 d.f.).

The results of the fecundity study are shown in table 4 and figure 2. Of the statistics shown, the mean and range figures provide the basis for age group comparison, and the standard deviation and the standard error of the mean are presented merely as points of additional interest. Differences between the numbers of fish reported in table 4 or figure 2 and those reported in the original sample are due to the omission of aberrant specimens (2 females, 1 each in 1957 and 1959, had but a single ovary) and those fish whose ages were indeterminable because of scale erosion.

Examination of table 4 or figure 2 discloses that the egg content of individual fish within an age group sample varied by as much as 2,749 eggs. Little between-year variation is evident for the means of a single group. The variation between the means of the 4_2's and the 5_3's, different age groups having similar ocean age, is also small.

TABLE 3.—*Estimated and actual egg counts of a randomly selected subsample, 1957–59*

Fish No.	Estimated count	Actual count	Difference
1	1,695	1,773	−78
2	2,007	1,958	49
3	2,118	2,018	100
4	3,067	3,027	40
5	4,272	4,088	184
6	2,581	2,304	277
7	2,094	2,074	20
8	1,611	1,697	−86
9	2,823	3,000	−177
10	1,906	1,759	147
11	2,038	2,000	38
12	1,872	1,852	20
13	2,002	1,984	18
14	2,840	2,706	134
15	3,662	3,562	100
16	2,678	2,920	−242
17	2,488	2,608	−120
18	2,676	2,560	116
19	3,237	3,183	54
20	3,437	3,300	137
21	3,172	3,055	117
Total	54,276	53,428	2,254
Average	2,584.57	2,544.19	40.38

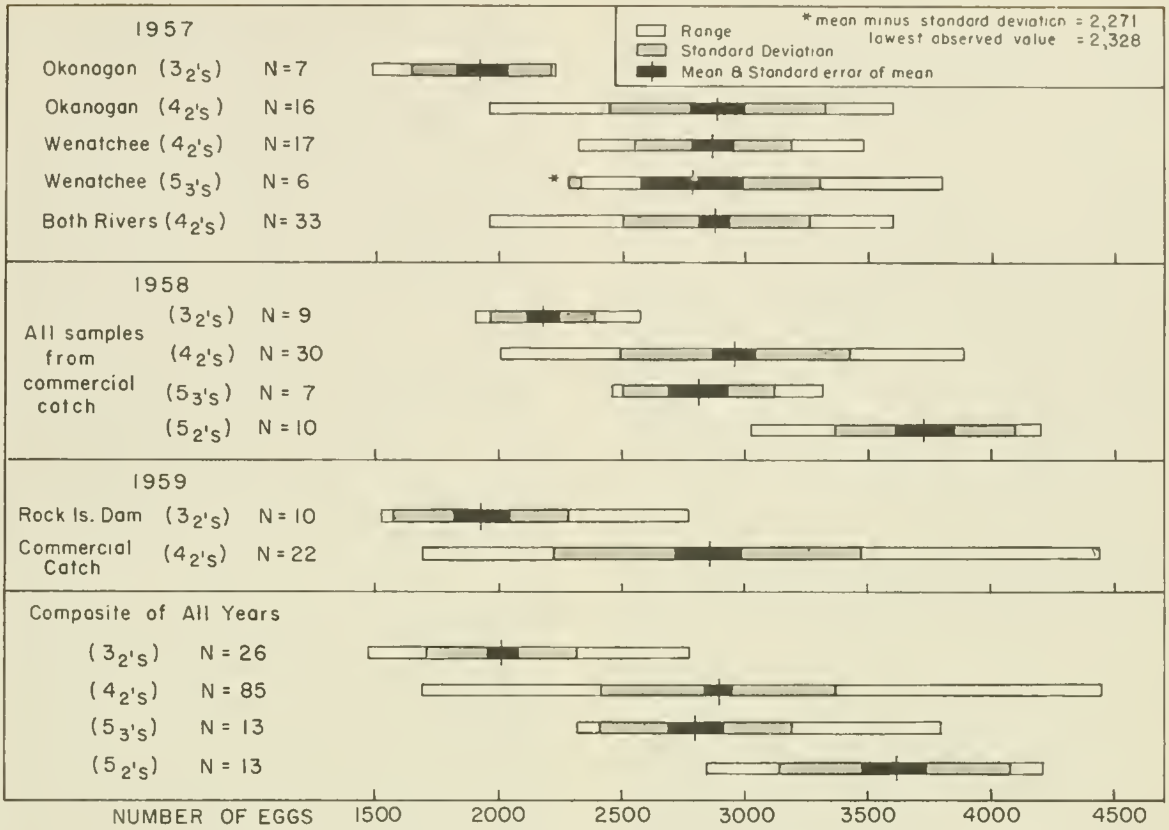

FIGURE 2.—Fecundity statistics of the blueback salmon age group samples.

TABLE 4.—*Fecundity statistics of the age-group samples of Columbia River blueback salmon 1957–59*

Sample		Fecundity information					
Year	Location	Age group	Number	Mean	Standard deviation	Standard error of the mean	Range
1957	Okanogan	3_2	7	1,928	283.93	107.31	1,478–2,216
	Do	4_2	16	2,887	437.03	109.26	1,958–3,593
	Wenatchee	4_2	17	2,871	317.05	76.90	2,314–3,481
	Do	5_3	6	2,890	512.89	209.43	2,328–3,799
	Both rivers	4_2	33	2,879	374.63	65.21	1,958–3,593
1958	All samples from commercial catch	3_2	9	2,172	214.84	71.61	1,900–2,574
		4_2	30	2,952	464.42	84.79	1,999–3,884
		5_3	7	2,811	302.90	114.47	2,454–3,319
		5_2	10	3,731	369.64	116.90	3,034–4,206
1959	Rock Island Dam	3_2	10	1,931	358.57	113.40	1,526–2,774
	Commercial catch	4_2	22	2,851	625.85	133.44	1,697–4,446
All years		3_2	26	2,014	306.71	60.15	1,478–2,774
		4_2	85	2,897	477.13	51.75	1,697–4,446
		5_3	13	2,801	394.46	109.39	2,328–3,799
		5_2	13	3,609	465.96	129.22	2,847–4,206

The most striking feature is the within-year difference in mean fecundity between age groups with different ocean age. The mean fecundity of the 3_2's was lower than that of the 4_2's by 33, 26, and 32 percent for the years 1957, 1958, and 1959, in that order. On a similar basis we find that the 1958 3-year-ocean females (5_2's) averaged 26 percent more eggs than the dominant 4_2 age group for that year. The 3-year means of fecundity were 2,014, 2,897, 2,801, and 3,609 for the 3_2, 4_2, 5_3, and 5_2 age groups, respectively.

Variations in the measuring techniques and in the sampling sites cast sufficient doubt on the validity of the fork-length data to preclude their extensive use. For that reason we have limited the analysis to comparison of age group means.

We recognize that such comparisons are less sensitive than comparison by analysis of covariance but feel, nevertheless, that the means, usually derived from stratified samples, fairly represent the age groups.

Effect of Age Group Fecundity and Sex Ratio on Egg Potential

Our second specific objective is to assess the effect of age and sex composition on the egg potential of Okanogan River spawning escapements. Using the estimated age and sex composition (table 5)[3] and the age group fecundity information, we have calculated the egg potential of the Okanogan River spawning escapements of 1953 and 1956 through 1959 in three ways:

Estimate (A) is based on the number of fish in the escapement and on the assumptions of an even sex ratio and a mean fecundity of 3,000 eggs per female.

Estimate (B) is based on the number of females in the escapement and on the assumption of 3,000 eggs per female.

Estimate (C) is based on the number of females in each age group and the mean fecundity of the age groups present.

It is clearly evident from the results (table 6) that the effect of age and sex composition on the egg potential of the Okanogan River blueback spawning escapements varies widely from year to year. In 1957 and 1959 the individual variables offset one another and resulted in little over-all change in estimated egg potential. In sharp contrast, the combined influence of the two factors reduced the estimated egg potential by 43, 24, and 60 percent in 1953, 1956, and 1958, respectively.

When we consider the variables separately to determine their relative importance we see that sex ratio was the most important factor in 1956, 1958, and 1959, whereas age group fecundity was the greater source of error in 1953 and 1957.

To illustrate the combined effect of sex ratio and age group fecundity on egg potential and ultimately on escapement-return relationships, let us compare from table 6 the three measures of egg potential for the years 1957 and 1958. Using estimate (A), we note that the egg potential in 1958 was 1.24 times as large as that of 1957. From these data we might expect the return from the 1958 brood to be 1.24 times as great as the return from the 1957 brood, all other factors affecting the return being similar.

Correcting for the numbers of female spawners in each age group and the mean fecundity for each age group (estimate C), we note that the egg potential in 1958 is only about one-half the egg potential in 1957. Other factors affecting the return being similar, we might expect that the return from the 1958 escapement would be only one-half as large rather than 1.24 times as large as the return from the 1957 escapement.

By the same reasoning, we would expect that the 1953 escapement would produce a return only one-half as large as would an escapement of the same size, but normal with respect to age and sex composition.

We fully realize that the escapement-return relationship of 1953–57 would have been poor

TABLE 5.—*Estimates of the age and sex composition of the Okanogan River blueback spawning populations 1953, 1956–59*

Year	Spawning ground estimate	Number in sample	Number and percentage—							
			In each age group		Of each sex					
			3_2	4_2	3_2		4_2		Both	
					Males	Females	Males	Females	Males	Females
1953	34, 260	216	29, 669 (87)	4, 591 (13)	16, 971 (57)	12, 698 (43)	3, 323 (72)	1, 267 (28)	20, 295 (59)	13, 965 (41)
1956	39, 256	323	9, 775 (25)	29, 481 (75)	6, 383 (65)	3, 392 (35)	16, 244 (55)	13, 237 (45)	22, 627 (58)	16, 629 (42)
1957	25, 350	695	7, 630 (30)	17, 720 (70)	5, 074 (67)	2, 556 (33)	6, 751 (38)	10, 969 (62)	11, 825 (47)	13, 525 (53)
1958	31, 035	208	26, 100 (84)	4, 935 (16)	21, 324 (82)	4, 776 (18)	1, 944 (39)	2, 991 (61)	23, 268 (75)	7, 767 (25)
1959	40, 650	326	6, 098 (15)	34, 552 (85)	3, 232 (53)	2, 866 (47)	14, 581 (42)	19, 971 (58)	17, 813 (44)	22, 837 (56)

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[3] Because the 3_2's are rarely found in streams other than the Okanogan, we believe that the discrepancies between the number of small fish (3_2's) counted at Rock Island Dam (table 1) and the 3_2's in the estimated Okanogan population (table 5) are due to (1) errors in the spawning ground estimates, (2) errors in the large-small breakdown at Rock Island Dam, and (3) mortalities that occur between the two sites.

TABLE 6.—*Estimated egg potential of Okanogan blueback salmon escapement using three methods of estimation, 1953 and 1956–59*

[In millions of eggs]

Year	Method		
	A	B	C
1953	51	42	29
1956	59	50	45
1957	38	41	37
1958	47	23	19
1959	61	69	62

compared with other years, regardless of the influence of 1-year-ocean fish. This indicates that other factors also affect the relationship. We have shown specifically, however, that the presence of abnormal numbers of 1-year-ocean females reduced the egg potential of the 1953 Okanogan escapement to a level well below that expected of a run similar in size but normal in age and sex composition. Although the impact of 1-year-ocean females would have been relatively less in terms of the riverwide escapement, we feel that initial overestimation of the egg potential accentuated the poor escapement-return relationship of 1953–57. It is evident that future analyses of the Columbia River blueback escapement-return data can be improved initially by refining the escapement statistic with the added consideration of sex ratio and age group fecundity.

DISCUSSION

Thus far, we have considered the effect of the lower fecundity of 1-year-ocean fish on the egg potential of a spawning stock and have pointed out that, because of fluctuations in relative abundance of 1-year-ocean fish in the escapement, the egg potential is sometimes considerably less than the number of spawners or even female spawners indicates. It is appropriate to examine other aspects of the occurrence of these 1-year-ocean fish in the Columbia River blueback runs, including their direct and indirect importance to the fishery and the cause of their occurrence.

Contribution of 3_2's to the Fishery

Lack of sustained yearly information about the composition of the escapement at Bonneville Dam hinders efforts to calculate the exploitation rate of the various age groups. The Oregon Fish Commission[4] reports that in 1957 the fishery took 9 percent of the 3_2 age group as compared to 52 percent of the 4_2 age group. The 3_2's thus contribute little to the catch but are heavily represented in the escapement. Their relative significance on the Okanogan spawning grounds is further increased by the fact that they return, almost without exception, to that stream. By reason of sheer abundance then, the 3_2's often contribute heavily to the egg potential of the Okanogan escapement. Utilizing the number of female spawners in each group and the appropriate average fecundity of each age group, we calculate that the 3_2's contributed 88, 15, 14, 54, and 9 percent of the total egg potential for the years 1953, and 1956 through 1959, respectively.

Because the 3_2's are relatively invulnerable to the gill net fishery as it is now conducted and, therefore, contribute significantly to the reproductive capacity of the Okanogan escapements, they might be considered as a safety factor in the escapement to that river system. The apparent advantages of such a feature would be nullified, however, if the recurrence of the 3_2's were genetic in nature. For the 3_2's to function beneficially as a safety factor, they must be able to produce catchable 4_2's as well as 3_2's. Otherwise, the contribution of the Okanogan River blueback populations to the commercial fishery would, in time, be eliminated.

Age at Maturity—Genetic or Environmental?

The question of whether age at maturity of Pacific salmon is the result of environmental or genetic influence or a combination of the two has only recently attracted attention. Godfrey (1958) working with sockeye salmon at Rivers Inlet and Skeena River, B.C. (Canada), concludes that "age at maturity is governed to a great extent by the inheritance of certain genetic components of the parents. Some environmental influence is a possibility but must be proven."

On the Deschutes River in Washington States 3-year-old chinook salmon (*O. tshawytscha*) females were crossed with 2- and 3-year-old males, separately to determine whether or not precocious parents tend to produce precocious offspring

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[4] Westrheim, S. J., and others. 1959. Columbia River investigations progress report October 1957–April 1958. Oregon Fish Commission (Portland), February, 1959, 54 p. Processed.

(Washington Department of Fisheries, 1959). The cross that involved the 2-year-old male produced a significantly larger number (168) of 2-year-old fish than did the cross that involved the 3-year-old male (79).

Ricker [5] using Adams River, B.C. (Canada) data, found that "observed differences between broods, in age of males at maturity is strongly influenced by the age of their fathers."

Certain evidence, on the other hand, seems to minimize the role of genetics in the recurrence of precocious blueback salmon: (1) the lack of a significant correlation between the 1-year-ocean bluebacks of year n and those of year n+3; (2) the scarcity of these small fish in the Wenatchee system. In 1939–43, the years of the Grand Coulee Relocation Program, blueback salmon were intercepted at Rock Island Dam and transported to Lakes Osoyoos and Wenatchee (Fish and Hanavan, 1948). Although exact data are lacking, generally as many small 1-year-ocean fish were placed in the Wenatchee as in the Okanogan system. Were the recurrence of 3_2's entirely genetic, we could normally expect a continuation of the strain in each system. The absence of 1-year-ocean fish in the Wenatchee runs suggests that the conditions in that system simply did not lend themselves to the production of 1-year-ocean fish. This aspect of the problem is clouded, however, by the lack of knowledge concerning the kokanee-blueback [6] relationship.

Another question concerned with the function of the 3_2's as a safety-factor is that of the relative survival of eggs and progeny resulting from small females. The ability of the small females to bury the eggs deep enough to protect them from physical rigors is also subject to speculation.

CONCLUSIONS

Female Columbia River blueback salmon that spawn after spending only one year in the ocean contain roughly one-third fewer eggs than normal 2-year-ocean females.

Escapements to the Okanogan spawning tributary exhibit wide annual fluctuations in age and sex composition. Abnormal numbers of 1-year-ocean females can greatly reduce the egg potential of a particular escapement and, in turn, distort the escapement-return relationship involving that brood.

The unusually high incidence of 1-year-ocean fish in the 1953 Okanogan escapement reduced the egg potential to about one-half that expected of an escapement similar in size but normal in age and sex composition. It appears this initial overestimation of egg potential may have accentuated the relatively poor riverwide escapement-return relationship of 1953–57.

Although the 1-year-ocean fish have a lower fecundity and contribute little directly to the commercial fishery as it is now conducted, they may, by virtue of their contribution to reproduction, have a positive value as a safety factor in the escapement.

Further assessment of the value of 1-year-ocean fish requires more exact knowledge about (a) the role of genetics in the recurrence of the 3_2's, (b) the relative survival of eggs deposited by large and small females, and (c) the relative viability of progeny produced by 2-year-ocean parents, 1-year-ocean parents, and combinations of both.

SUMMARY

Although 1-year-ocean fish are common in the spawning escapements of the Columbia River blueback salmon, their contribution to the reproductive capacity of an escapement has not previously been assessed.

The need for assessment became evident when the 1953 Rock Island escapement, which contained unprecedented numbers of 1-year-ocean fish, failed to produce a total run in 1957 that exceeded itself.

A fecundity study, conducted from 1957–59, revealed that the 1-year-ocean females contained 33, 26, and 32 percent fewer eggs than the 2-year-ocean fish in those years, respectively. The pooled-means of numbers of eggs per female were 2,014 for 1-year-ocean fish and 2,897 for 2-year-ocean fish.

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[5] Ricker, W. E. Evidence for environmental and genetic influence on certain characters which distinguish stocks of the Pacific salmons and steelhead trout. Fisheries Research Board of Canada, Nanaimo, B.C. Unpublished manuscript, 1959.

[6] Individuals of the species that complete their entire life cycle in fresh water.

Three methods were used to estimate the egg potential of 1953 and 1956 through 1959 Okanogan River escapements. The first method was based on the assumptions that one-half of the estimated spawners were females and that the average egg content per female was 3,000 eggs. Method 2 had as its base the observed number of female spawners and an average fecundity of 3,000. The third and most refined method was based on the number of females in each age group and the average fecundity of each age group.

Comparison of the results of the three methods shows that failure to correct for sex ratio and fecundity when estimating the reproductive capacity of an escapement can seriously distort the accuracy of the escapement statistic for use in escapement-return analyses.

The high incidence of small females in the 1953 Rock Island escapement substantially reduced the egg potential normally expected of an escapement of that size. This distortion of the escapement statistic accentuated the poor escapement-return relationship of 1953–57.

LITERATURE CITED

Fish, Frederic F., and Mitchell G. Hanavan.
1948. A report from the Grand Coulee fish-maintenance project 1939–1947. U.S. Department of Interior, Fish and Wildlife Service, Special Scientific Report No. 55. 63 p.

Gangmark, Harold A., and Leonard A. Fulton.
1952. Status of Columbia River blueback runs, 1951. U.S. Department of Interior, Fish and Wildlife Service, Special Scientific Report—Fisheries No. 74. 29 p.

Gilbert, Charles H., and Willis H. Rich.
1927. Investigations concerning the red-salmon runs to the Karluk River, Alaska. U.S. Bureau of Fisheries, Bulletin, vol. 43, Part 2, p. 1–69.

Godfrey, Harold.
1958. A comparison of sockeye salmon catches at Rivers Inlet and Skeena River, B.C., with particular reference to age at maturity. Journal Fisheries Research Board of Canada, vol. 15, No. 3, p. 331–354.

Nelson, Philip R.
1959. Effects of fertilizing Bare Lake, Alaska, on growth and production of red salmon (*O. nerka*). U.S. Fish and Wildlife Service, Fishery Bulletin, vol. 60, No. 159, p. 59–86.

Washington (State) Department of Fisheries.
1959. 69th Annual Report, Year 1959. 243 p. Seattle.

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DETERMINING AGE OF YOUNG HADDOCK FROM THEIR SCALES

By ALBERT C. JENSEN and JOHN P. WISE

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ABSTRACT

The history of age determinations of haddock from various areas is discussed, with a résumé of the previous work in New England and adjacent areas. Various methods of validation of age determination of haddock in New England waters are considered and evaluated. It is concluded that scales provide a satisfactory indication of the age of these fish, particularly for their first 5 years.

DETERMINING AGE OF YOUNG HADDOCK FROM THEIR SCALES

By Albert C. Jensen and John P. Wise, *Fishery Research Biologists*

BUREAU OF COMMERCIAL FISHERIES

Haddock *Melanogrammus aeglefinus* (Linnaeus) are distributed over the continental shelves of the eastern and western North Atlantic Ocean and are the basis for large and valuable fisheries on both sides of the ocean (table 1). In the United States, an economically important fishery for the species has existed since 1925, which contributes to the livelihood of many people living in or near several New England ports, particularly those of Massachusetts.

TABLE 1.—*U.S. and world landings of haddock, dressed fresh (FAO 1959)*

[In thousands of metric tons]

Year	United States	World (including United States)
1953	63. 3	294. 3
1954	70. 3	343. 7
1955	61. 3	396. 2
1956	69. 1	430. 8
1957	60. 6	408. 9
1958	54. 2	371. 5

The fish is a member of the cod family, Gadidae, but is easily distinguished from the cod or any of the other closely related gadids by the black shoulder spot and black lateral line. Bigelow and Schroeder (1953) give a detailed description of the haddock, its habits and habitats, but a few key points in its life history are outlined below.

The haddock is a demersal fish and, except for the spawning period when feeding diminishes, spends its life moving over the ocean floor in search of food. Spawning takes place near the bottom from February to May, with the peak of spawning in March and April. After the eggs are fertilized, they rise and float near the surface of the sea, drifting with the current. An egg hatches in about 14 days, and the larva, which is about 5 millimeters long, continues to drift with the current.

When young haddock are about 4 to 5 months old and 10 to 13 centimeters long, they begin to descend to the ocean floor, where they will spend the rest of their lives.

During their pelagic existence haddock feed on plankton, but as adults on the bottom (Wigley, 1956) their food consists largely of slow-moving invertebrates found on or burrowing in the substratum. Food items vary according to location and season, but in general consist of crabs, shrimps, snails, worms, starfish, sea urchins, sand dollars, and sea cucumbers. Haddock eat squid and occasionally feed on fish, mostly sand lance (*Ammodytes*), but fishes form only a very small part of their diet.

Haddock do not grow to the large sizes attained by cod. They rarely exceed 85 to 90 cm. in length; the largest haddock on record is an Icelandic fish 111 cm. long. Sexual maturity is reached when the fish are about 40 cm. long and 3 years old (Clark, 1959).

The New England fishery for haddock is concentrated on Georges Bank, one of a series of fishing banks which lie off the coast of northeastern United States and eastern Canada. Georges Bank (Schuck, 1951), bounded on three sides by the 100-fathom isobath, has its center about 150 miles east of Cape Cod. The haddock are fished for by a fleet of otter trawlers, the majority of which land their catches in Boston, Mass. The fish are landed in two market categories, "scrod," weighing between 1½ and 2½ pounds (gutted weight); and "large," weighing more than 2½ pounds (gutted weight).

NOTE.—Approved for publication May 2, 1961. Fishery Bulletin 195.

THE NEED FOR AGE DATA

In 1930, the Bureau of Fisheries (now the Bureau of Commercial Fisheries, U.S. Fish and Wildlife Service) began an investigation to determine (1) what caused the decline of the haddock fishery in waters fished by U.S. vessels, (2) what could be done to increase the abundance of haddock, or at least to prevent further decline in the catch, and (3) what predictions of future catches were possible.

To carry out the objectives of the investigation, large quantities of data have been and still are collected at important haddock ports (Boston, Gloucester, and New Bedford, Mass.; Rockland and Portland, Maine). Collections have been made routinely at Boston since the early 1930's, and were started later at the other ports.

The background for the collection of these data is reported by Rounsefell (1948). The data include almost complete records of the poundages landed from the various banks, with records of depths and locations from which the fish were taken, the gear used, and the days spent in fishing. Concurrent with this collection, random samples of the lengths of fish in the landings and selected samples of scales were also collected. For our studies, haddock were measured from the tip of the snout to the fork of the tail. About 30,000 fish were measured in 1959 and 3,500 scale samples were collected from an estimated 24 million haddock landed.

The data are analyzed primarily to determine the fluctuations in haddock abundance. Age determinations from scale readings are also used in special studies of the natural and fishing mortality rates, growth rate, and age composition of the catch.

To process the mass of biostatistics and to maintain a smooth flow of information relating to the age composition of the fishery, a quick and reliable method of age determination is needed. Scales have been used for 20 or more years at this laboratory. They are easily removed from the fish and it is possible to measure several hundred fish and take scale samples in a relatively short time at the port. The scales are easily processed in the laboratory; scales from 100 fish, for example, can be processed and read in about 1 man-day. The purpose of the present paper is to document the techniques originally used to validate the scale-reading method of haddock age determination and to present later studies of the usefulness of the method.

PREVIOUS STUDIES

Fishery biologists on both sides of the North Atlantic have for many years determined the ages of haddock from interpretation of scale markings. The publications of many of the workers report age compositions and growth rates but do not validate the method by which the scale ages were determined (cf. Huntsman and Needler, 1927; Schuck and Arnold, 1951; Wise, 1957; Kohler and Clark, 1958). Other workers have reported not only their results but, in addition, have described their methods of interpreting scale age determinations. These papers are of great interest in the present study.

In a study of haddock in Norwegian waters, Saetersdal (1953) reports that in many investigations haddock ages have been determined from scale examinations without testing the validity of the method. He then proceeds to demonstrate the validity of age determination methods for the Norwegian stocks of haddock, using the Petersen method. He points out that part of the year class of fish under observation failed to form a scale annulus in the second year. He also examined the secular record of the scales, including the time of annulus formation, and concluded, "* * * the zones found in * * * the scales were annual formations in the great majority of the cases."

In North American waters, several workers have used haddock scales for age determination. Among them, Needler (1929) used scale readings to derive growth rates for haddock from Lockeport, the Sable Island banks, and St. Andrews (Canada). He states categorically, "The age of haddock may be determined from the scales." and cites Thompson (1923) for his validation of haddock scale readings. (Thompson had examined the scales of North Sea haddock and found that 95 percent of the scales gave what he believed to be the correct age.)

In a later study Needler (1930) read haddock scales for age determination of fish from the Gulf of Maine and Georges Bank and again cited other workers for his proof of the scale method. He concluded, "There can be no doubt of the validity

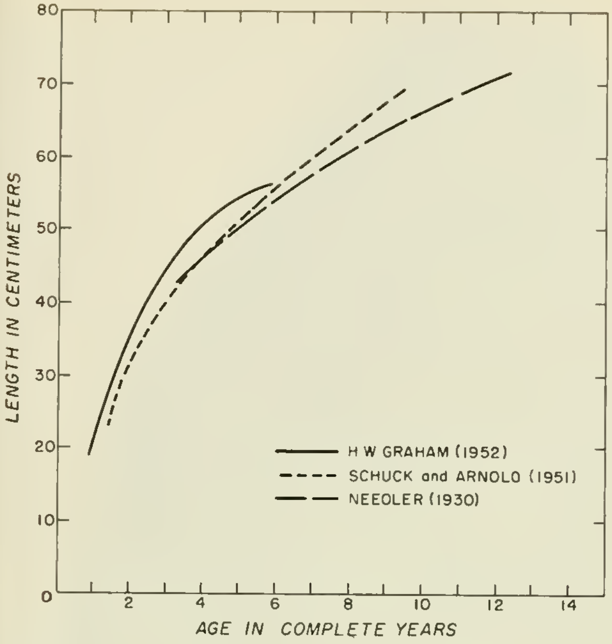

FIGURE 1.—Growth curves for Georges Bank haddock.

of the method, although inaccuracies are bound to occur."

In the 1930 report, Needler derived a growth curve for Georges Bank haddock, based on scale readings from 189 fish collected during May–September 1927. The growth curve is shown in figure 1, and on it we have indicated age-length values derived by Schuck and Arnold (1951) and H. W. Graham's (1952) growth rate. Graham's (1952) age-length data were taken from February 1 (completed year) scale readings. Both Needler (1930) and Schuck and Arnold (1951) obtained their age-length data from mid-year scale readings, thus the length for each age includes additional growth. Figure 1 indicates that Needler, Schuck and Arnold, and H. W. Graham do not differ markedly in their age determinations.

Recently, the more specific problems encountered in aging Georges Bank haddock have been studied by Jensen and Clark (1958), who determined the time of annulus formation on haddock scales; Clark (1958), who reported on the consistency with which different scale readers read the same scale samples; and Kohler and Clark (1958), who reported comparisons of age determinations from otoliths and scales from the same sample of haddock. These recent studies warrant closer examination and will be discussed in detail below.

Our haddock biostatistical data show that in past years more than 80 percent of Georges Bank haddock are caught by the time they have completed their fourth year. Furthermore, we are more confident about our age determinations of young fish. The annuli are most sharply defined in the scales of haddock 2, 3, and 4 years old, and the difference between summer growth and winter growth is very marked (Jensen and Clark, 1958). Needler (1930) noted this, too, when he stated: "In the later years in the life of the haddock, the annual zones become very narrow and the number of circuli in each small. In many of these cases the age is truly an 'estimation,' whereas the age of younger individuals can more truly be said to be 'determined.'"

Our own investigations bear this out, and Kohler and Clark (1958) report no statistically significant differences between scale and otolith ages up to about 7 years; after the seventh year, scale readings are consistently lower than otolith readings.

VALIDATION OF THE SCALE READING METHOD

Haddock scales are cycloid and oval to elliptical in shape (fig. 2). They do not show radii or transverse grooves, sometimes present on cycloid scales from other species. The external surface is sculptured with concentric circuli arranged about the focus, but the internal surface is relatively featureless. The focus is usually anterior to the center of the scale, but occasional scales are found with the focus at the center. Periods of rapid and slow growth are indicated by the spacing of the circuli. In studies of several species of gadids, including the haddock, J. S. Thomson (1904) noted that "* * * the growth of scales is cyclical or periodic, and * * * the rings formed thereby are annual."

J. S. Thomson considered temperature as a factor in forming annual rings only as it affects the food supply. He suggested that the scale circuli are widely spaced during the period of rapid growth in the warm season when food is plentiful and closely spaced during the period of slow growth in the cold season when food is scarce. Cutler (1918) believed water temperature to be the direct cause of annual rings. In an aquarium study with flounder and plaice, he concluded the food supply determined the number of circuli,

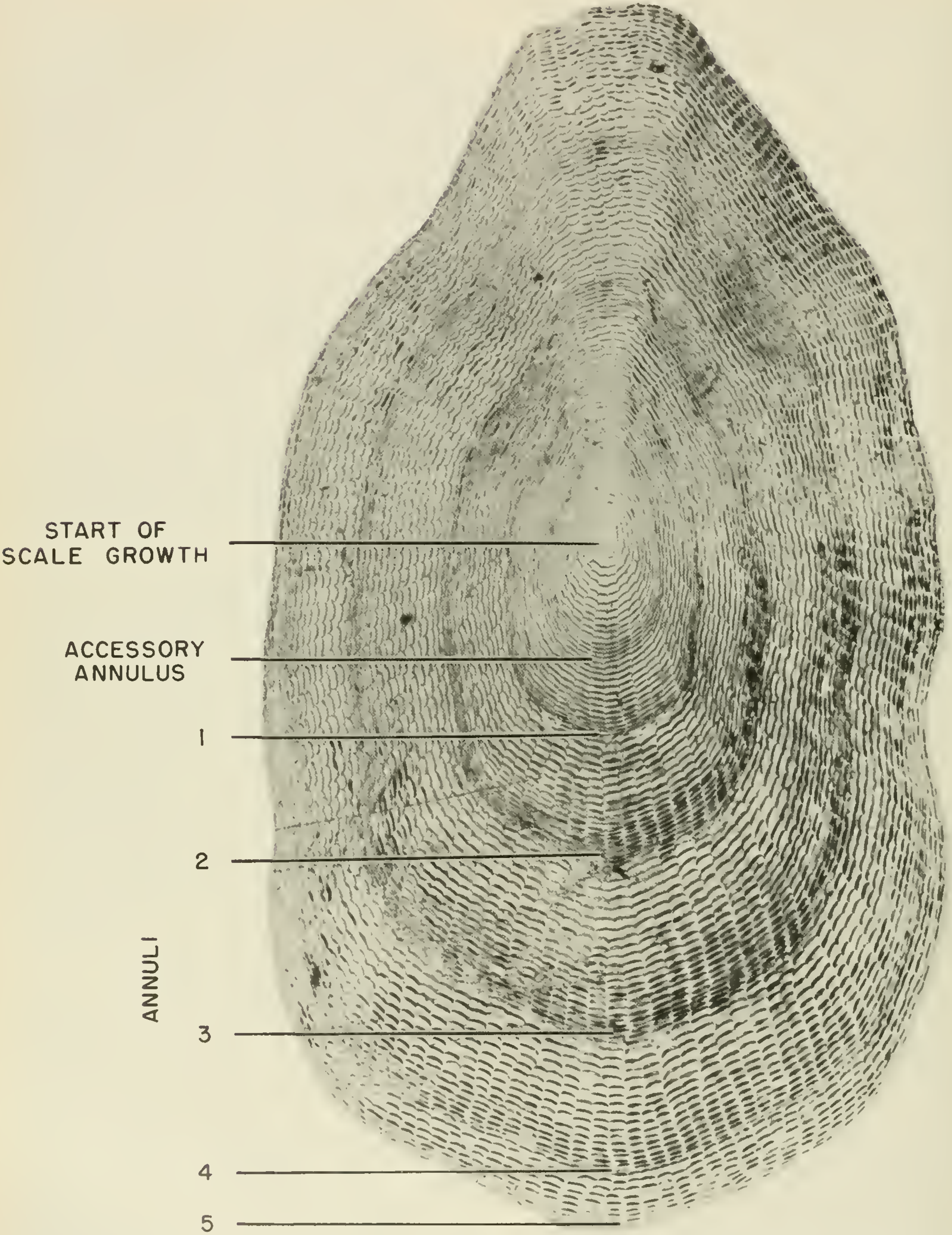

FIGURE 2.—Plastic impression of a scale from a 5-year-old haddock. Five annuli and the accessory annulus are visible.

but the water temperature determined the spacing between circuli. Lee (1920) notes that narrow "sclerites" begin to form on haddock scales in August or earlier, when the water temperature is increasing. She suggests that at this time the fish may be migrating into the cooler offshore waters where the decreased temperature produces the closely spaced circuli or "winter rings."

The role of food and feeding and their effects on haddock scale zones have not been clearly demonstrated, although some indirect evidence has been accumulated. Narrowly spaced circuli generally form on the scales of Georges Bank haddock in the period August–April (Jensen and Clark, 1958). For haddock from Nova Scotia offshore banks, Homans and Vladykov (1954) report November through May to be a season of diminished feeding. The period of least feeding coincided with the spawning period (February, March, and April) while the months of June through October constituted the feeding season. For Georges Bank haddock, Wigley (1956) reports that during the spawning period a decline in feeding, rather than a complete cessation, takes place, and for the period of annulus formation, the average volume of food per haddock rose from 1.8 cubic centimeters in September to 3.0 cubic centimeters in January but was lowest (1.0 cubic cm.) in February. We can see no clearcut evidence, based on Wigley's data, that diminished feeding causes the formation of narrowly spaced circuli.

There seems no reasonable doubt that widely spaced circuli are formed in summer and narrowly spaced in winter, whatever the direct cause. For the purpose of this study the point of interest is that zones are laid down on the scales at the rate of one for each winter and one for each summer, the two zones making a pattern which indicates a single year's interaction of the haddock and its environment.

Haddock Scale Reading Procedure

The annulus used by us in haddock age determinations is the zone of closely spaced circuli. It has the following characteristics:

1. It is concentric with the margin of the scale.
2. It can be traced, by careful scrutiny if necessary, entirely around the scale.
3. It is clearly separated from other such zones and does not ordinarily meet them at any point.
4. If present, it is on all the normal scales of an individual.

The scales from scrod haddock are thin and readily transmit light. Therefore, they are placed dry on a glass slide and examined under a binocular microscope with substage illumination. Large haddock scales are thicker and do not readily transmit light. To overcome this, large haddock scales are routinely impressed in plastic slides as described by Arnold (1951). The impressions are projected with a commercial microprojector at a magnification of about 40×. A minimum of three scales are examined from each fish. Regenerated and deformed scales are discarded.

The number of complete annuli, from the focus to the posterior edge of the scale, is counted to determine the age of the fish in years. The annulus is considered complete on February 1 (the arbitrary "birthday" of Georges Bank haddock), selected because most of the haddock commence spawning in February.

Results from a study of the formation of scale zones of Georges Bank haddock (Jensen and Clark, 1958) have shown that one annulus is formed each year. This was demonstrated by a predominance of widely spaced circuli at the scale edge during May–July and a predominance of narrowly spaced circuli during August–April.

Problems in interpreting scales arise because of the ambiguity of some annuli. For example, in a routine sample of scales from 510 Georges Bank haddock, read by the senior author, only 100 (19.6 percent) had distinct, well-separated annuli and were considered by him as easy to read. The fish were 1 to 5 years old and the annuli were sharply defined. The remaining 80 percent of the scales required detailed study to determine the age.

The most frequent error in scale reading probably arises from counting an accessory annulus usually found in the first zone of broad circuli (fig. 2). Thompson (1923) has termed this annulus a "false winter appearance" and suggests it occurs when the young haddock first descend to the bottom and their growth is checked as they enter the deep cold water. Our studies have shown that this accessory annulus occurs in slightly less than 50 percent of the scales examined for age determination.

We had an opportunity to examine critically the nature of the accessory annulus while doing some scale back-calculations for another study. We examined 513 scales collected in February and March, 1956 and 1957, from Georges Bank haddock, 3 to 6 years old. The scales had been collected as part of the routine port sampling program and represented a typical sample of scales used in our age determination procedure. In the sample of 513 scales, 245 (47.8 percent) showed an accessory annulus. A random subsample of 38 scales was taken for a more detailed study of the accessory annulus. Back calculations were made on the subsample to obtain these data: (1) L_1—calculated fish length at the end of the first year; (2) L_a—calculated fish length when the accessory annulus first began to form; (3) L_b—calculated fish length when the accessory annulus was complete; (4) C_a—number of circuli from the focus to the first narrow circulus in the accessory annulus; and (5) C_b—number of circuli from the focus to the last narrow circulus in the accessory annulus (see table 2).

TABLE 2.—*Calculated fish length-scale length relationship for accessory mark on Georges Bank haddock scales*

Age at capture	Fork length (mm.)	L_1 (mm.)	Accessory mark			
			L_a (mm.)	L_b (mm.)	C_a	C_b
3 years old	423	201	118	135	11	16
	432	359	108	120	9	11
	429	210	111	143	10	18
	425	180	101	112	9	11
	451	187	111	135	10	17
	438	232	128	146	12	17
	430	184	119	145	10	16
	458	183	128	146	12	18
	417	178	125	150	11	19
	402	174	114	131	11	18
	422	201	109	143	12	22
	465	202	130	166	11	22
	320	160	100	120	10	18
	397	186	98	118	9	14
4 years old	456	197	141	162	11	16
	503	214	107	148	7	16
	399	171	124	142	12	17
	418	198	130	145	10	14
	509	188	121	138	9	13
	483	222	118	140	10	14
	468	201	138	158	12	15
	501	192	100	114	7	11
	533	151	89	103	5	8
	446	140	89	102	6	9
	459	170	110	128	9	14
	445	237	145	165	11	17
	462	185	115	131	11	14
	406	200	128	161	12	21
	504	212	121	152	12	21
	484	203	130	149	11	18
	522	204	103	134	6	8
5 years old	572	262	123	161	8	14
	579	185	110	141	10	18
	600	197	116	142	12	18
6 years old	633	178	118	139	11	17
	522	188	91	129	8	20
	597	191	89	129	6	20
	503	165	122	145	11	15
Mean		197	115	139	10	16

The accessory annulus starts to form when the haddock attain an average length of 115 mm. and is complete when the haddock attain an average length of 139 mm. The accessory annulus consists of about seven closely spaced circuli within a zone of widely spaced circuli and includes the 10th through the 16th circulus from the focus. Broadly spaced circuli, denoting rapid growth, are found on the scale after the accessory mark and are in turn followed by a zone of narrow circuli. This zone of narrow circuli is the first true annulus and is considered complete on February 1, although a few additional narrow circuli are formed in February and March. The accessory annulus usually is well separated from the first true annulus and with training and experience can be readily recognized by the scale reader.

Another source of error may arise from mechanical damage to the scale. The exposed posterior edges of some scales, particularly from fish more than 7 years old are ragged and appear to be eroded, suggesting that some annuli may be missing.

Confirmation of Ages from Length Distributions

Comparing the ages read from scales with the modal peaks in a length distribution of a sample of fish (the Petersen method) helps to confirm the scale method and particularly helps to establish the time of formation of the first true annulus. Haddock scale readings were thus confirmed by Duff (1916) for haddock from St. Andrews, by Saetersdal (1953) for Norwegian haddock, and by Schuck and Arnold (1951) for haddock from Browns and Georges Banks.

Figure 3 shows mean lengths of young-of-the-year haddock collected by us in 1957 on Georges Bank and in the Gulf of Maine. The term "young-of-the-year haddock" includes those fish that have not yet completed the first year of life. As explained previously, the year is considered complete on February 1. Small haddock, such as are represented in these data, are difficult to collect in sufficient quantities at one time for detailed length-distribution analysis. Therefore, the various collections were incorporated into one series of data in table 3.

Collections of larval fish, made aboard the *Albatross III* in April 1957, contained haddock

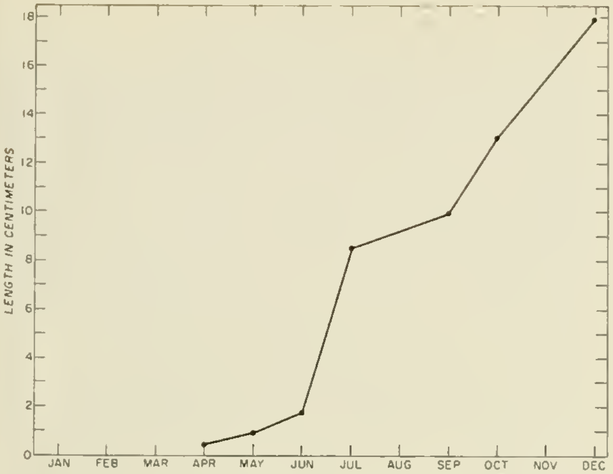

Figure 3.—Mean lengths of young-of-the-year haddock collected on Georges Bank and in the Gulf of Maine in 1957.

averaging 4.5 mm. long. Presumably these fish had been spawned only 1 or 2 weeks previously. In collections made in May 1957, postlarval haddock, averaging 9.6 mm. long, were taken. In June, young haddock 18.0 mm. long were collected at or near the surface but by July, the haddock had grown to an average length of 85.8 mm. and were in the middepths, mostly at 20 meters.

Midwater trawling from the *Albatross III* in September caught young haddock, average length 99.2 mm., slightly deeper in the middepths, presumably moving down to begin their existence on the sea bottom.

In a collection of juvenile haddock, made with a one-half-inch mesh otter trawl in October and November 1957, the fish averaged 132.0 mm. It is at this time that most haddock scales form the accessory annulus discussed previously.

The December collection represents juvenile haddock taken by a commercial otter trawler. The young-of-the-year haddock now average 179.0 mm. in length and have almost attained their full first year's growth. The average length for the December sample agrees well with the average length of 196 mm. for 1-year-old fish in the data.

Table 3.—*Length composition of young-of-the-year haddock collected on Georges Bank and in the Gulf of Maine in 1957*

Length (cm.)	April	May	June	July	Sept.	Oct.	Dec.
0.3	1	----	----	----	----	----	----
0.4	11	----	----	----	----	----	----
0.5	7	----	----	----	----	----	----
0.6	3	----	----	----	----	----	----
0.7	----	2	----	----	----	----	----
0.8	----	3	----	----	----	----	----
0.9	----	2	3	----	----	----	----
1.0	----	4	----	----	----	----	----
1.1	----	2	----	----	----	----	----
1.2	----	3	----	----	----	----	----
1.3	----	----	1	----	----	----	----
1.4	----	----	----	----	----	----	----
1.5	----	----	----	----	----	----	----
1.6	----	----	----	----	----	----	----
1.7	----	----	----	----	----	----	----
1.8	----	----	1	----	----	----	----
1.9	----	----	----	----	----	----	----
2.0	----	----	2	----	----	----	----
2.1	----	----	----	----	----	----	----
2.2	----	----	----	----	----	----	----
2.3	----	----	----	----	----	----	----
2.4	----	----	----	----	----	----	----
2.5	----	----	----	----	----	----	----
2.6	----	----	----	----	----	----	----
2.7	----	----	----	----	----	----	----
2.8	----	----	----	----	----	----	----
2.9	----	----	----	----	----	----	----
3.0	----	----	1	----	----	----	----
3.1	----	----	----	----	----	----	----
3.2	----	----	----	----	----	----	----
3.3	----	----	----	----	----	----	----
3.4	----	----	1	----	----	----	----
3.5	----	----	----	----	----	----	----
3.6	----	----	----	----	----	----	----
3.7	----	----	----	----	----	----	----
3.8	----	----	----	----	----	----	----
3.9	----	----	----	----	----	----	----
4.0	----	----	----	11	----	----	----
5.0	----	----	----	20	2	----	----
6.0	----	----	----	33	----	----	----
7.0	----	----	----	16	3	----	----
8.0	----	----	----	24	6	----	----
9.0	----	----	----	17	23	2	----
10.0	----	----	----	51	61	1	----
11.0	----	----	----	50	37	17	----
12.0	----	----	----	9	4	50	----
13.0	----	----	----	----	----	70	----
14.0	----	----	----	----	----	39	----
15.0	----	----	----	----	----	19	1
16.0	----	----	----	----	----	16	----
17.0	----	----	----	----	----	5	4
18.0	----	----	----	----	----	----	2
19.0	----	----	----	----	----	----	2
20.0	----	----	----	----	----	----	2
21.0	----	----	----	----	----	----	----
22.0	----	----	----	----	----	----	----
23.0	----	----	----	----	----	----	----
24.0	----	----	----	----	----	----	----
25.0	----	----	----	----	----	----	----
N=	22	16	9	231	136	219	11
Mean=	0.45	0.96	1.80	8.52	9.93	13.23	17.91

An earlier collection of 419 haddock scales and length measurements was made on Georges Bank during *Albatross III* cruise 56 (Feb. 1–13, 1955) (table 4 and fig. 4). The length frequency of these fish shows distinct modes at 18, 30, and 42 cm. Examination of the scales revealed that all of the 14 haddock that measured from 11 to 21 cm. (the first mode) had one annulus. More than 61 percent of the 105 haddock from 22 to 36 cm. (the second mode) had 2 annuli, while most of the remaining 39 percent of this size group had 3 such marks. The third mode was composed mostly (more than 71 percent) of fish with 3 annuli.

If haddock spawned throughout the year, a length-frequency curve of the population would

TABLE 4.—*Age composition of 419 Georges Bank haddock, by 3-cm. groups*

Length (cm.)	Age group (number of complete annuli)									Total
	1	2	3	4	5	6	7	8	9+	
12	1	----	----	----	----	----	----	----	----	1
15	4	----	----	----	----	----	----	----	----	4
18	6	----	----	----	----	----	----	----	----	6
21	3	----	----	----	----	----	----	----	----	3
24	7	----	----	----	----	----	----	----	----	7
27	----	15	1	----	----	----	----	----	----	16
30	----	33	----	----	1	----	----	----	----	34
33	----	13	14	----	----	----	----	----	----	27
36	----	4	17	----	----	----	----	----	----	21
39	----	2	40	4	----	----	----	----	----	46
42	----	----	52	8	----	----	----	----	----	60
45	----	----	40	8	2	----	----	----	----	50
48	----	----	28	5	4	----	----	----	----	37
51	----	----	13	6	7	6	1	----	----	33
54	----	----	1	2	9	4	1	----	----	17
57	----	----	----	1	12	7	3	----	----	23
60	----	----	----	----	4	6	1	1	----	12
63	----	----	----	----	2	4	1	1	----	8
66	----	----	1	----	----	----	2	2	----	5
69	----	----	----	----	----	1	1	1	----	3
72	----	----	----	----	----	1	2	----	2	5
75	----	----	----	----	----	----	----	----	1	1
Mean length	19.6	30.5	42.4	46.0	53.8	57.7	62.0	64.8	73.0	------

consist of an irregular line with its highest point near the ordinate and sloping downward to the right. But haddock spawn in one relatively brief time of the year; the young from a single year's spawning are about the same size and form a mode in a length-frequency graph. The small fish are the young fish; i.e., fish represented by the first mode have no annulus or only one annulus on their scales. Fish represented by the second or third modes have two or three annuli, respectively, on their scales.

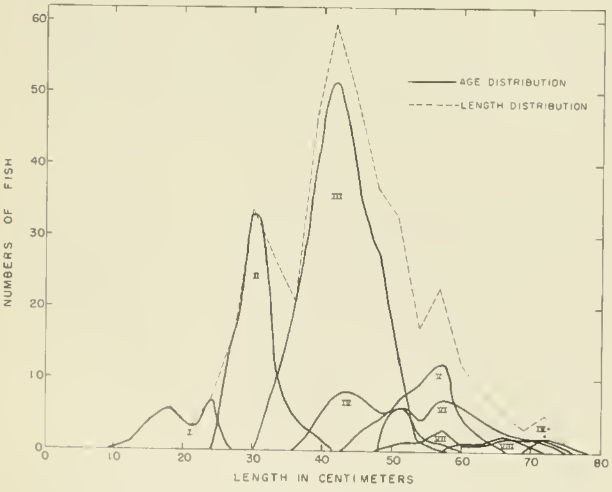

FIGURE 4.—Age analysis of the length composition of 419 Georges Bank haddock collected on *Albatross III* cruise 56, February 1955.

Confirmation from Age Distributions

Long-term observations of a fish population when the age frequencies are plotted will show the progression of strong year classes through the fishery, but this test only demonstrates that the majority of age readings are correct and is not meaningful unless the stock is adequately sampled (M. Graham, 1929). The year-class progression becomes less valuable when the outstanding year classes cease to be dominant and when the scales of the older fish become difficult to read.

In general, dominant year classes remain dominant in an age-frequency histogram for the first few years. Unfortunately, the stronger year classes appear to lose their dominance (in age frequency) in later years. This is due, no doubt, both to errors in scale reading and to differing mortality rates.

Year-class progression is demonstrated in the graph of the catch per day, by age, of Georges Bank haddock landed at Boston from 1948 through 1957 (fig. 5) and represents scale readings from 42,000 haddock. The relative strengths of several year classes are also shown. For example, the 1948 year class of haddock was very large and is well represented by the catch of 2-year-old fish in 1950. The 1948 year class also dominated the landings as 3-year-olds in 1951 and were well represented as 4-year-olds in 1952. However, in 1952, the 1948 brood is about equal in strength to the less successful 1949 brood, and by 1953 it is subordinate to the 1949 brood.

Similarly, the 1950 year class formed a large part of the catch as 2-year-olds in 1952 and as 3-year-olds in 1953. The 1951 year class was relatively poor, but the 1952 year class appeared in large numbers in the landings as 2-year-olds in 1954 and as 3-year-olds in 1955.

These observations tend to support the validity of our age readings. It will be noticed, however, that these strong year classes appear to lose their dominance after about the fourth year. Whether this is due to differential mortality or to age reading error, or both, remains to be resolved.

Comparison of Scales and Otoliths

A detailed study of haddock scale-otolith comparisons was reported by Kohler and Clark (1958) who examined material from 764 Georges Bank and Nova Scotia fish 1 to 13 years old. The two

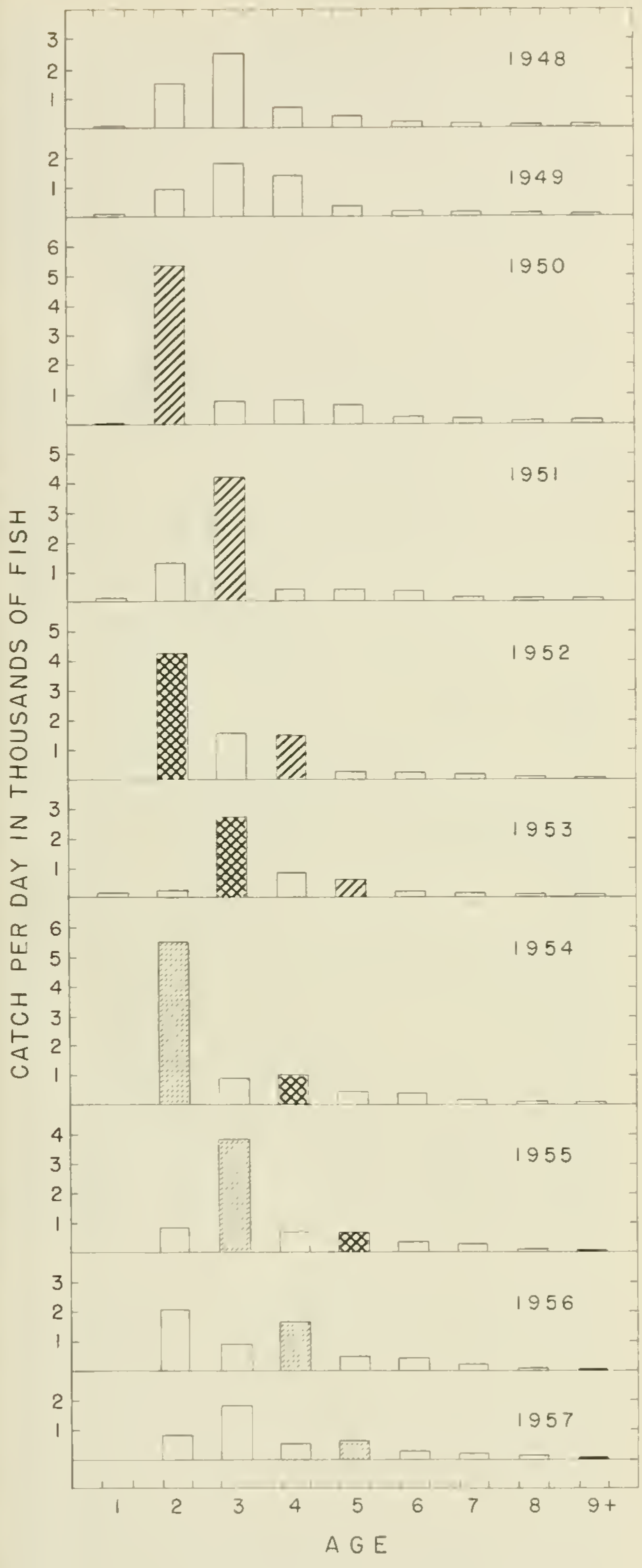

FIGURE 5.—Catch per day of haddock taken in Georges Bank Fishery.

methods agreed in 62 percent of the cases, but closer agreement (73 percent) was obtained when only fish 2 through 5 years old were examined.

M. Graham (1929) has stated that scale-otolith comparisons do not prove the validity of either method unless it is demonstrated that the periodic zones are formed simultaneously on both the scales and otoliths. Such comparisons may serve as indices to the validity of one method if it is supported by the other method.

Confirmation from Tagging

The recapture of marked fish of known age is the most direct means to validate age determinations, since the time parameter is precisely known. The technique is essentially this: the fish are marked and, before they are released, scales are removed for age determination. When a marked fish is recaptured, a second age determination is made and compared with the first. Since the time at liberty is known, any growth can be directly compared to time.

To examine this growth, scales were taken at the time of recapture from 32 tagged haddock and compared with scales taken from the same fish at the time of tagging. The fish were at liberty from 9 to 150 weeks. The scales were examined as follows: "at return" and "at tagging." Scales from each fish were impressed on plastic slides (64 in all). Each slide was identified only by a code number and the month in which the scale sample was taken. All of the slides were examined independently by two experienced scale readers, who marked the annuli for each scale on a card. When the readings were completed, the markings on the cards were compared to determine whether both readers had interpreted the same zones as annuli. Both sets of scales were identically interpreted for 29 of the 32 fish (table 5); the 3 questionable sets were re-examined by both readers together. Two of the fish in question had not formed identifiable annuli for one of their years at liberty; one was at liberty for 105 weeks and the other for 150 weeks. On the scale of the third fish, a zone was identified as an annulus by one of the readers but not by the other. This zone was formed immediately following tagging and perhaps resulted from interruption of growth caused by capture and tagging. It is significant

TABLE 5.—*Comparison of scales from 32 tagged haddock*

Month and year		Weeks at large	Age		
Haddock tagged 1954–58	Recaptured 1954–59		Tagged	Recaptured	Expected
April 1954	July 1954	13	7	7	7
Do	August 1954	14	7	7	7
Do	October 1954	26	3	3	3
Do	December 1954	33	4	4	4
Do	April 1955	50	4	5	5
Do	July 1955	63	4	5	5
Do	do	63	4	5	5
Do	do	65	4	5	5
Do	September 1955	72	4	5	5
Do	May 1956	105	4	5	6
Do	February 1957	150	4	6	7
August 1954	October 1954	9	2	2	2
Do	January 1955	25	4	4	4
Do	March 1955	31	6	7	7
Do	do	31	4	5	5
Do	May 1955	39	4	5	5
Do	June 1955	46	5	6	6
Do	October 1955	64	4	5	5
Do	January 1956	74	5	6	6
July 1956	March 1959	139	3	6	6
October 1957		32	3	4	4
Do	May 1958	49	1	2	2
November	August 1958	49	3	4	4
Do	September 1958	54	4	5	5
Do	November 1958	55	4	5	5
Do	do	63	4	5	5
Do	January 1959	68	5	7	7
Do	February 1959	69	3	5	5
Do	March 1959	72	3	5	5
March 1958	August 1958	20	6	6	6
Do	do	21	5	5	5
Do	February 1959	49	7	8	8

that these "tagging-checks" were not discovered by either reader on scales of any of the other fish.

DISCUSSION

The formation of an annulus on fish scales may be caused by one or more extrinsic or intrinsic factors such as temperature changes or physiological cycles.

Lee (1920) has suggested that haddock form annuli when they migrate from one environmental temperature to another. We know from marking experiments that Georges Bank haddock are relatively sedentary and the thermal milieu on Georges Bank does not vary greatly through the year. It is probable then that the annuli are not caused by marked differences in water temperature.

It might be argued that the scale annuli are spawning checks. The physiological drain in producing large amounts of gametes may cause formation of closely spaced circuli on the scales. As stated, previously, this zone of circuli is the annulus counted in haddock age determinations. The period of annulus formation (August to April) begins almost 7 months prior to the beginning of spawning and 5 to 6 months prior to the maturation and ripening of the sex products. Annuli are also seen on the scales of small, sexually immature fish and could not then have been caused by spawning activities.

Scale annuli may be caused by diminished feeding; a decline in feeding during the spawning season is reported by Wigley (1956). His data for April (height of spawning) are for a group of 256 fish whose average length is 35 cm. Such fish are almost all immature (Clark, 1959), and their reduced feeding intensity probably is due to a cause other than spawning activity.

What causes the formation of the annulus is not definitely known. But not knowing the cause does not remove the effect; annuli, formed once each year, are present on the scales and indicate a consistent annual phenomenon.

Consistency of age determinations is sometimes cited in arguments supporting validity of the determinations. Two or more people reading the same sample of scales and getting the same ages may be a result of (1) their having been trained in one set interpretation of the zones and thus reading the scales "with the same eyes," or (2) using independent interpretations of obvious scale markings. If the readers are using the same interpretation, their readings should agree. If they are using somewhat different interpretations, their readings will agree closely, but not completely. The agreement of haddock scale readers is very close (89 percent to 93 percent agreement in our laboratory) between individuals and with repeated readings by the same individual. This high degree of consistency shows only that the scale markings are usually clear and easily read.

Another consideration is the progression of strong year classes through the fishery as shown by the modes of age-frequency histograms (fig. 5). When a mode advances by 1 year with the passage of 1 year, it shows that the year class represented by the mode has also increased 1 year in age.

When the scales of tagged fish are studied, it might be argued that tagged fish show a "tagging" check on the scale presumably caused by the tagging operation. Following this line of reasoning, the scale-determined age should be 1 year more than the chronological age for recovered tagged fish. It has been shown that most tagged haddock produce one scale annulus per year, and the scales from 29 of the 32 tagged fish mentioned earlier showed only one additional annulus for each year at liberty. It is reasonable to assume, therefore, that haddock, at least, do not form a tagging check. Despite the lack of volume of recapture information, the available data are favorable to the use of scales from tagged fish as a test of age validation since the scales at recapture had grown (either in number of edge circuli or in the total number of annuli) while the tagged fish was at liberty.

CONCLUSIONS

1. Haddock ages determined by scale readings were compared with ages judged from length-frequency curves (Petersen method). The two sets of age determinations were in very close agreement for the first 3 years (100 percent for the first year, 61 percent for the second year, and 71 percent for the third year). Beyond the third year the length-frequency modes are obscured by overlapping of the lengths for each age.

2. The zone of closely spaced ("winter" type) circuli considered to be the annulus is formed during the period August through April. Only one annulus is formed during the year.

3. Age determinations from haddock scales read by different readers agreed in about 90 percent of the readings. The scale annuli are usually clear and easy to read.

4. Ages read from scales and from otoliths for the same fish agreed in 62 percent of the cases for a sample of 764 fish, 1 to 3 years old. Closer agreement (73 percent) resulted from the readings for fish 2 to 5 years old.

5. When catch-per-day data by age class for commercial haddock landings were plotted each year for 10 years, peaks representing outstanding year classes stood out from the adjacent poorer year classes. These peaks could be followed from year to year.

6. From a total of 32 tagged fish, an increase in the number of annuli equal to the number of years at liberty was noted in 29 fish. Scales from 2 fish had fewer annuli than years at liberty: one fish was in the ocean 2 years, but grew only one annulus; the other fish was in the ocean 3 years and grew 2 annuli.

7. Georges Bank haddock-scale annuli are formed one each year; they are true year zones and age determinations from these scales are valid in most of the haddock.

LITERATURE CITED

Arnold, Edgar L., Jr.

1951. An impression method for preparing fish scales for age and growth analysis. Progressive Fish-Culturist, vol. 13, No. 1, p. 11–16.

Bigelow, Henry B., and William C. Schroeder.

1953. Fishes of the Gulf of Maine. U.S. Fish and Wildlife Service, Fishery Bulletin, No. 74, vol. 53, p. 1–577.

Clark, John R.

1958. Consistency of scale reading. International Commission for the Northwest Atlantic Fisheries, Special Publication No. 1, p. 191–192.

1959. Sexual maturity of haddock. Transactions of the American Fisheries Society, vol. 88, No. 3, p. 212–213.

Cutler, D. Ward.

1918. A preliminary account of the production of annual rings in the scales of plaice and flounders. Journal of the Marine Biological Association of the United Kingdom, N.S., vol. 11, No. 4, p. 470–496.

Duff, Dorothy.

1916. Investigation of the haddock fishery, with special reference to the growth and maturity of the haddock (*Melanogrammus aeglefinus*). Contributions to Canadian Biology for 1914–1915, Sessional Paper No. 38a, p. 95–102.

Food and Agricultural Organization of the United Nations.

1959. Yearbook of Fishery Statistics, vol. 9, section C., p. 20–25. Rome, Italy. [Distributed by United Nations, New York.]

Graham, Herbert W.

1952. Mesh regulation to increase the yield of the Georges Bank haddock fishery. International Commission for the Northwest Atlantic Fisheries, Second Annual Report, Part 3, p. 23–33.

Graham, Michael.

1929. Studies of age-determination in fish. Part II. A survey of literature. Ministry of Agriculture and Fisheries, London, Fisheries Investigations, series II, vol. 11, No. 3, p. 1–50.

Homans, R. E. S., and V. D. Vladykov.

1954. Relation between feeding and the sexual cycle of the haddock. Journal of the Fisheries Research Board of Canada, vol. 11, No. 5, p. 535–542.

Huntsman, A. G., and A. W. H. Needler.

1927. Fluctuations in the haddock fishery of the Bay of Fundy. Contributions to Canadian Biology and Fisheries, N.S., vol. 3, No. 18, p. 425–436.

Jensen, Albert C., and John R. Clark.

1958. Time of formation of scale annuli. International Commission for the Northwest Atlantic Fisheries, Special Publication No. 1, p. 193–197.

Kohler, A. C., and J. R. Clark.

1958. Haddock scale-otolith comparisons. Journal of the Fisheries Research Board of Canada, vol. 15, No. 6, p. 1239–1246.

Lee, Rosa M.

1920. A review of the methods of age and growth determination in fishes by means of scales. Ministry of Agriculture and Fisheries, London. Fisheries Investigations, series II, vol. 4, No. 2, p. 1–2.

Needler, A. W. H.

1929. Studies on the life history of the haddock (*Melanogrammus aeglifinus* Linnaeus). Contributions to Canadian Biology and Fisheries, N.S., vol. 4, No. 20, p. 267–285.

1930. The migrations of haddock and the interrelationships of haddock populations in North American waters. Contributions to Canadian Biology and Fisheries, N.S., vol. 6, No. 10, p. 241–313.

Rounsefell, George A.

1948. Development of fishery statistics in the North Atlantic. U.S. Fish and Wildlife Service, Special Scientific Report No. 47. 18 p.

Saetersdal, Gunnar S.

1953. The haddock in Norwegian waters. II. Methods in age and growth investigations. Report on Norwegian Fishery and Marine Investigations, vol. 10, No. 9. 46 p.

Schuck, Howard A.

1951. Studies of Georges Bank haddock. Part I. Landings by pounds, numbers, and sizes of fish. U.S. Fish and Wildlife Service, Fishery Bulletin, No. 66, vol. 52, p. 151–176.

Schuck, Howard A., and Edgar L. Arnold, Jr.

1951. Comparison of haddock from Georges and Browns Banks. U.S. Fish and Wildlife Service, Fishery Bulletin, No. 67, vol. 52, p. 177–185.

Thompson, Harold.

1923. Problems in haddock biology with special reference to the validity and utilization of the scale theory. I. Preliminary Report. Scientific Investigations, Fisheries Division, Scotland, No. 5, p. 1–78.

Thomson, J. Stuart.

1904. The periodic growth of scales in gadidae as an index of age. Journal of the Marine Biological Association of the United Kingdom, N.S., vol. 7, No. 1, p. 1–109.

Wigley, Roland L.

1956. Food habits of Georges Bank haddock. U.S. Fish and Wildlife Service, Special Scientific Report—Fisheries No. 165. 26 p.

Wise, John P.

1957. Growth rate of Browns Bank haddock. U.S. Fish and Wildlife Service, Research Report 50. 13 p.

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DEVELOPMENT, DISTRIBUTION, AND COMPARISON OF RUDDER FISHES *Kyphosus sectatrix* (Linnaeus) and *K. incisor* (Cuvier) IN THE WESTERN NORTH ATLANTIC

BY DONALD MOORE

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ABSTRACT

Synonymies are listed for *Kyphosus sectatrix* and *Kyphosus incisor*, the two species studied. Development of these species is described and illustrated from the smallest juvenile to the largest adult examined (*K. sectatrix*, 115 specimens from 10.4 to 260 millimeters, standard length; and *K. incisor*, 99 specimens ranging 8.5–252 mm.). All specimens examined were from the North Atlantic Ocean, and most were from the Atlantic coast of the United States and the Bahama Islands north of lat. 23°30′ N. No abrupt changes in rate of development of selected characters occurred with increase of size. However, a gradual decrease in rate of development with increase in size was indicated in many of the characters.

The reported distribution of both species along the Atlantic coast of the United States and the northern Bahamas is reviewed and revised, with the northern reported range for *K. incisor* extended to Cape Cod. Lenth-frequency data indicate an extended spawning season for both species. Scale and pectoral fin-ray counts indicate that few specimens taken in the Gulf Stream came from the northern Bahamas.

The two species are similar except for total dorsal and anal soft-ray counts and gill-raker counts. Scale and pectoral-ray counts indicate that the *K. sectatrix* taken at Bermuda and in the northern Bahamas are not part of the population found along the Atlantic coast of the United States. A key is provided to aid in separating the two species.

DEVELOPMENT, DISTRIBUTION, AND COMPARISON OF RUDDER FISHES *Kyphosus sectatrix* (Linnaeus) and *K. incisor* (Cuvier) IN THE WESTERN NORTH ATLANTIC

By DONALD MOORE, *Fishery Research Biologist*,

BUREAU OF COMMERCIAL FISHERIES

Between January 1953 and December 1954 the U.S. Fish and Wildlife Service, in cooperation with the U.S. Navy Hydrographic Office, the Office of Naval Research, the Georgia Game and Fish Commission, and the Florida State Board of Conservation (through the Marine Laboratory, University of Miami), collected data and samples along the south Atlantic coast of the United States and in the northern Bahama Islands on nine cruises of the motorship *Theodore N. Gill* (Anderson, Gehringer, and Cohen, 1956 a, b; and Anderson and Gehringer, 1957 a, b; 1958 a, b; 1959 a, b, c). During identification of the specimens collected by dipnet on these cruises, it became apparent that the juveniles of the two species of the genus *Kyphosus* (family Kyphosidae) reported from the North Atlantic Ocean were, in many instances, not readily distinguishable from one another.

Meek and Hildebrand (1925) in their report on the *Kyphosus* in Panama said,

> * * * The affinities of the Atlantic coast species are, however, not well understood and we cannot be certain of the identification of the specimens at hand. We have compared our specimens with others from North Carolina, Florida, Bermuda, and Cuba. Unless there is much variation among individuals with respect to the depth of body, number of anal and dorsal rays, and number of scales in a lateral series, there must occur on the Atlantic coast more than two species of this genus, the number recognized in current works. * * * A close study of a large amount of material from the Atlantic would be very desirable.

Later publications do not clarify the identification of the species of *Kyphosus* in the North Atlantic; also the development of young of these species has not previously been described.

This paper presents a review of the taxonomy and the results of a study on the development, distribution, and comparison of the two species of rudder fishes, *Kyphosus sectatrix* (Linnaeus) and *Kyphosus incisor* (Cuvier), found along the Atlantic coast of the United States and the northern Bahamas.

Young rudder fishes are available as forage for other fish, and adults are considered to be excellent game and food fish. Mowbray (1949) said of *K. sectatrix*: "Probably the most potentially important small game fish of Bermuda waters is the chub, or rudder fish as it is sometimes known. This fish is found in large numbers amongst the reefs surrounding the island and it rivals the bonefish in gameness, and surpasses it in strength. The average weight of a chub is about eight pounds though they reach twenty."

I am grateful for the assistance given by various staff members and to those who loaned me specimens: Leonard P. Schultz, U.S. National Museum; E. Milby Burton, Charleston Museum; University of Florida Museum; and David K. Caldwell, Brunswick, Georgia; and for information given by Paulo de Miranda Ribeiro.

METHODS AND DEFINITIONS

Measurements of 15 mm. or greater were made with drafting dividers and a Paragon scale; those measurements greater than 50 mm. were recorded to the nearest 0.5 mm. while those from 15 mm. to 50 mm. were recorded to the nearest 0.1 mm. Measurements less than 15 mm. were made with a micrometer eyepiece on a stereoscopic microscope, and recorded to the nearest 0.1 mm. Drawings of fishes, and of caudal osteology, were made with the aid of a camera lucida.

Original measurements were used in the plots of body proportions to standard length. Unless otherwise stated, specimen lengths are standard length measurements. Stained specimens were prepared using the methods described by Hollister (1934) and Evans (1948).

NOTE:—Approved for publication May 24, 1961. Fishery Bulletin 196.

DEFINITIONS OF TERMS

Standard length.—Distance from tip of snout to posterior border of hypural bones. (All measurements from tip of snout are with mouth closed and do not include any anterior protrusion of incisor teeth in adults.)

Eye diameter.—Horizontal width of the orbit.

Head length.—Distance from tip of snout to posterior fleshy margin of opercle.

Body depth at pelvic fin.—Distance from base of pelvic spine to base of first dorsal spine.

Snout to dorsal fin.—Distance from tip of snout to base of first dorsal spine.

Snout to anal fin.—Distance from tip of snout to base of first anal spine.

Snout to pectoral fin.—Distance from tip of snout to insertion of first pectoral ray.

Snout to pelvic fin.—Distance from tip of snout to base of pelvic spine.

Pectoral fin length.—Distance from insertion of first pectoral ray to tip of fin with fin pressed to side of specimen.

Spine.—A fin ray which is relatively inflexible, is unsegmented or becomes unsegmented during development and does not have flattened tip. (Counts are listed by roman numerals.)

Soft-ray.—A fin ray which is relatively flexible, is segmented or becomes segmented during development and usually has a flattened or branched tip. (In caudal fin the counts are listed: dorsal plus ventral.)

Teeth.—Counts given are for one side of one jaw.

Gill rakers.—(1) Entire first arch—total number, including tubercles, on the first gill arch on one side. (2) Upper limb—total on epibranchial bone in first arch excluding raker at angle. (3) Lower limb—total on ceratobranchial and basibranchial bones in first arch including raker at angle. (4) Ceratobranchial bone—total on bone in first arch including raker at angle and any others partly attached to this bone (frequently one raker at junction of the ceratobranchial and basibranchial bones is only partly attached to the ceratobrancial).

Scales.—(1) Row above lateral line—counted in the row above the lateral line, to base of caudal rays. (2) Straight line—counted along the continuous horizontal row which terminates one row below the lateral line at the caudal peduncle, small scales at cleithrum excluded.

Atlantic coast of the United States.—Along the Atlantic coast from Eastport, Maine, to Dry Tortugas Islands, Florida, including the Florida Current to the Bahama Islands.

Northern Bahamas.—The Bahama Islands lying north of Latitude 23°30′ North.

MATERIAL

Measurements and counts of selected parts were recorded from 115 specimens of *Kyphosus sectatrix* ranging from 10.4 to 260 mm. (table 1), and from 99 specimens of *Kyphosus incisor* ranging from 8.5 to 252 mm. (table 2). The specimens of *Kyphosus* at the Biological Laboratory, Brunswick, Ga., ranging from 8.7 to 54.5 mm., were supplemented by material ranging from 8.5 to 260 mm. from the U.S. National Museum, the Charleston Museum, the University of Florida Collections, and the Jamaica collection of David K. Caldwell.

KYPHOSUS SECTATRIX (LINNAEUS)

Perca saltatrix Linnaeus, 1758: p. 293 (Bahamas, Florida, or Carolina), misprint for *sectatrix* in Catesby, 1743: p. 8.

Perca sectatrix Linnaeus, 1766: p. 486 (Bahamas, Florida or Carolina), correction of misprint.

Chaetodon cyprinaceus (Broussonet) Gmelin, 1789: p. 1269 (tropical Atlantic).

Pimelepterus bosquii Lacépède, 1803: p. 429, pl. IX, fig. 1 (South Carolina).

Pimelepterus boscii Cuvier in Cuvier and Valenciennes, 1831: p. 258, pl. CLXXXVII (Carolina).

Pimelepterus oblongior Cuvier in Cuvier and Valenciennes, 1831: p. 264 (locality unknown).

Pimelepterus boscii var. *sicula* Doderlein, 1884: p. 83 (Gulf of Palermo).

Cyphosus bosqui Jordan, 1884: p. 128 (Key West, Florida).

Cyphosus elegans (*non* Peters) Metzelaar, 1919: p. 44 (Curacao, Venezuela).

Kyphosus palpebrosus Miranda Ribeiro, 1919: p. 176 (Isle of Trindade, Brazil).

Kyphosus metzelaari Jordan and Evermann, 1927: p. 506 (Curacao, Venezuela).

Kyphosus incisor (*non* Cuvier) Parr, 1930: p. 66 (Turks Island, British West Indies).

Kyphosus incisor (non Cuvier) Fowler, 1944: p. 87 (Roncador Bank, Colombia; off coast of Nicaragua).

Kyphosus lutescens (non Jordan and Gilbert) Carvalho, 1950: p. 116 (Isle of Trindade, Brazil).

Kyphosus sectator Tortonese, 1954: p. 82 (Palermo, Sicily).

The nomenclature of *Kyphosus sectatrix* (Linnaeus, 1766) has been decisive since Jordan and Gilbert (1883) noted that Lacépède had used the name *Kyphosus* for *Kyphosus bigibbus* (1802) earlier than *Pimelepterus*. Jordan and Gilbert (1883) also said: "The word should however be spelled with an initial C, as *Cyphosus*." Many subsequent authors made this change. Lacépède did not spell it with a "C," therefore, the correct name is *Kyphosus*.

The species *K. palpebrosus* Miranda Ribeiro (1919), taken at the Isle of Trindade, Brazil, is placed in synonymy with this species since the description of the type differs only slightly from the description of *K. sectatrix*. Measurements of selected parts of the 250-mm. holotype, taken

TABLE 1.—*Locations and dates of capture of 115 specimens of* Kyphosus sectatrix

[(BLBG) U.S. Bureau of Commercial Fisheries Biological Laboratory, Brunswick, Ga. (USNM) U.S. National Museum; (UF) University of Florida; (ChM) Charleston Museum]

Location	Date captured	Collection	Number of specimens	Size (mm.)
ATLANTIC COAST OF U.S. AND NORTHERN BAHAMAS:				
23°40′ N., 77°00′ W	Nov. 11–12, 1954	BLBG, *Gill* 9, Tongue of the Ocean	1	26.9
24°28′ N., 77°28′ W	Oct. 8, 1953	BLBG, *Gill* 4, Tongue of the Ocean	2	10.5
24°30′43″ N., 76°23′45″ W	Mar. 13, 1886	USNM 114775	3	19.4–34.0
Tortugas, Fla		USNM 116955	1	115.0
Do		USNM 116963	3	157.5–260.0
Nassau, Bahamas	Apr. 23, 1886	USNM 38433, *Albatross*	3	172.5–215.5
Angel Fish Creek, Fla. (South of Elliots Key)	December 1905	USNM 53302	1	125.0
Broad Creek, Fla. (South of Elliots Key)	Nov. 24, 1906	USNM 57173	1	211.0
Do	Dec. 15, 1905	USNM 53392	1	99.5
25°32′ N., 76°13′ W	Jan. 28, 1954	BLBG, *Gill* 5, Office of Naval Research	2	10.4, 36.2
26°20′ N., 76°43′ W	Jan. 24, 1954	BLBG, *Gill* 5, Std	1	12.0
26°21′ N., 76°44′ W	Jan. 23, 1954	do	1	26.4
26°23′ N., 76°46′ W	June 13, 1954	BLBG, *Gill* 7, Std	1	34.7
Key West, Fla		USNM 38729, *Albatross*	1	45.7
26°54′ N., 79°07′ W	Aug. 29, 1954	BLBG, *Gill* 8, Settlement Point, Bahamas	1	15.4
Jupiter Inlet, Fla	October 1958	UF 5950	1	22.5
27°37′ N., 79°40′ W	Oct. 12, 1953	BLBG, *Gill* 4, Reg. 6	1	15.0
27°38′ N., 76°23′24″ W	Feb. 24, 1886	USNM 114776	2	20.0, 30.8
29°00′ N., 79°48′ W	Oct. 14, 1953	BLBG, *Gill* 4, Reg. 15	1	13.1
Do	Apr. 27, 1954	BLBG, *Gill* 6, Reg. 15	1	11.3
29°10′ N., 80°19′ W	June 1, 1957	BLBG, *Combat* 336	2	18.7, 21.5
29°36′ N., 79°58′ W	Oct. 14, 1953	BLBG, *Gill* 4, Reg. 18	1	18.4
29°40′ N., 80°00′ W	Sept. 13, 1954	BLBG, *Gill* 8, Reg. 18	1	33.3
31°13′ N., 74°41′ W	June 13, 1903	USNM 53138	1	104.5
31°28′ N., 78°42′ W	Oct. 24–25, 1953	BLBG, *Gill* 4, Reg. 40	1	28.5
32°15′ N., 79°49′ W	Oct. 26, 1959	BLBG, *Silver Bay* 1388	1	52.0
32°18′ N., 77°29′ W	Oct. 26, 1953	BLBG, *Gill* 4, Reg. 51	1	26.8
32°24′ N., 79°28′ W	Oct. 26, 1959	BLBG, *Silver Bay* 1390	1	44.0
Charleston, S.C. (Pilot ship)	Sept. 18, 1938	ChM 38.210.2	4	39.6–71.6
Charleston, S.C	Sept. 4, 1938	ChM 38.207.5	2	36.1, 77.6
Magnolia Beach, S.C	September 1934	ChM 34.302.2	47	33.9–55.1
33°44′ N., 76°56′ W	Sept. 28, 1954	BLBG, *Gill* 8, Reg. 65	1	12.7
34°34′ N., 74°55′ W	Sept. 29, 1954	BLBG, *Gill* 8, Reg. 80	2	11.3, 13.2
Fort Macon Inlet, Beaufort, N.C	July 27, 1916	USNM 11752	6	25.6–39.6
38°25′ N., 72°40′ W	1885	USNM 101543	1	26.1
Woods Hole, Mass	Aug. 21, 1899	USNM 120580, *Fish Hawk*	1	133.0
MID NORTH ATLANTIC:				
Bermuda	1877	USNM 20177	1	154.5
Do	do	USNM 23543	1	236.0
Do	do	USNM 23544	1	194.0
Do	do	USNM 23545	1	171.0
Do	do	USNM 23546	1	168.0
CARIBBEAN SEA:				
Toro Point, Panama	Apr. 11, 1912	USNM 80668	1	244.0
Kingston, Jamaica, B.W.I. (Fish Market)	Apr. 21, 1959	D. K. Caldwell	1	230.0
Jamaica, B.W.I		USNM 37688	2	219.0, 259.0
Corrientes Bay, Cuba	Apr. 8, 1937	USNM 107431	1	100.5
West Indies	January 1885	USNM 131532	1	46.5
EASTERN NORTH ATLANTIC:				
Madeira		USNM 94528	1	211.0
Terceira, Azores	1894	USNM 94498	1	212.0

by Dr. Paulo de Miranda Ribeiro, August 28, 1959 (written communication), fell within the ranges found for *K. sectatrix*, except the eye diameter which was 6.8 percent of standard length. In my *K. sectatrix* above 150 mm., eye diameters ranged 7.5–10.2 percent of standard length.

The description of *K. incisor* by Parr (1930) has all the distinguishing features of *K. sectatrix*.

The description of *K. incisor* by Fowler (1944), which was later changed to *K. palpebrosus* by Fowler (1953), also has all the distinguishing features of *K. sectatrix*, including eye diameter.

The description of the specimen identified as *K. lutescens* by Carvalho (1950) from the Isle of Trindade, Brazil, is the same as that found for *K. sectatrix* except for the color and the number of scales. I found the color of *K. sectatrix* to be variable. Carvalho (1950) listed 98–101 scales, a count higher than that given for the holotype of *K. lutescens* by Jordan and Gilbert (1881) or for either *K. lutescens* or *K. sectatrix* by Jordan and Evermann (1898) [whom Carvalho (1950) used for comparisons]. Carvalho (1950) did not indicate the location of scales counted. I have not examined the relationship of the Pacific species *K. lutescens* with *K. sectatrix*.

The record of *K. sectator* Tortonese (1954) is of the same specimen named *Pimelepterus boscii* var. *sicula* by Doderlein (1884) which is placed in synonymy.

DEVELOPMENT

Dorsal fin.—X (6 specimens) or XI (54 specimens)—11 (4 specimens), 12 (100 specimens), or 13 (5 specimens) (table 3). Full complement of total dorsal rays (spines and soft-rays combined) is present by 10.4 mm. (see fig. 1, 10.5 mm.).

TABLE 2.—*Locations and dates of capture of 99 specimens of* Kyphosus incisor

[(BLBG) U.S. Bureau of Commercial Fisheries Biological Laboratory, Brunswick, Ga. (USNM) U.S. National Museum; (UF) University of Florida; (ChM) Charleston Museum.]

Location	Date captured	Collection	Number of specimens	Size (mm.)
ATLANTIC COAST OF U.S. AND NODTHERN BAHAMAS:				
23°40′ N., 77°00′ W	Nov. 11–12, 1954	BLBG, *Gill* 9, Tongue of the Ocean	1	19.2
24°04′ N., 79°15′ W	July 24, 1957	BLBG, *Combat* 448	4	10.2–14.5
Tortugas, Fla		USNM 116956	1	24.4
Do		USNM 116964	3	184.5–239.0
Nassau, Bahamas	Apr. 23, 1886	USNM 38433, *Albatross*	1	252.0
25°32′ N., 76°13′ W	Jan. 28, 1954	BLBG, *Gill* 5, Office of Naval Research	1	54.5
26°20′ N., 76°47′ W	June 13–14, 1954	BLBG, *Gill* 7, Std	1	17.2
26°23′ N., 76°48′ W	July 19, 1953	BLBG, *Gill* 3, Std	1	14.7
Martello Tower, Key West, Fla	July 3, 1919	USNM 111749	1	25.5
Cow Key, Key West, Fla	July 15, 1919	USNM 111748	1	28.6
26°37′ N., 79°51′ W	July 28, 1957	BLBG, *Cambat* 458	1	50.0
26°47′ N., 79°53′ W	do	BLBG, *Combat* 459	1	21.7
Palm Beach Inlet, Fla	June 9, 1958	UF 5918	1	29.7
Jupiter Inlet, Fla	July 6, 1958	UF Unsorted	1	17.6
Do	August 1958	UF 5981	1	19.9
Do	Dec. 21–24, 1958	UF (uncatalogued)	1	8.5
27°14′ N., 79°50′ W	July 29, 1957	BLBG, *Combat* 462	1	27.4
28°35′ N., 79°38′ W	June 10, 1958	BLBG, *Silver Bay* 447	1	17.5
29°00′ N., 77°00′ W	July 17, 1953	BLBG, *Gill* 3, Spc. 6	1	12.7
29°00′ N., 79°26′ W	Aug. 14, 1953	BLBG, *Gill* 4, Reg. 16	1	8.7
29°10′ N., 80°19′ W	June 1, 1957	BLBG, *Combat* 336	3	15.8–24.2
29°22′ N., 80°05′ W	Nov. 24, 1957	BLBG, *Silver Bay* 227	1	14.3
29°29′ N., 80°09′ W	Aug. 18, 1957	BLBG, *Combat* 485	1	33.6
29°29′ N., 80°10′ W	Aug. 19, 1957	BLBG, *Combat* 490	1	23.3
29°36′ N., 80°08′ W	Jan. 28, 1960	BLBG, *Silver Bay* 1620	1	21.2
29°38′ N., 79°36′ W	June 25, 1954	BLBG, *Gill* 7, Reg. 17	2	9.1.10.0
30°58′ N., 79°38′ W	Oct. 16, 1953	BLBG, *Gill* 4, Reg. 30	1	18.2
31°00′ N., 80°23′ W	do	BLBG, *Gill* 4, Reg. 32	3	16.7–28.4
31°00′ N., 80°46′ W	do	BLBG, *Gill* 4, Reg. 33	1	37.5
St. Simons Island, Ga	Oct. 5, 1955	BLBG	1	44.5
32°39′ N., 76°46′ W	Aug. 10, 1953	BLBG, *Gill* 3, Reg. 62	1	16.2
32°40′ N., 79°16′ W	Oct. 24, 1959	BLBG, *Silver Bay* 1372	9	23.4–31.0
Charleston, S.C. (Pilot ship)	Sept. 18, 1938	ChM 38.210.2	4	39.1–45.5
32°43′ N., 71°51′ W	Jan. 5, 1885	USNM 119766, *Albatross*	1	24.8
Charleston Harbor, S.C	Oct. 8, 1936	ChM 36.189.1	2	44.2, 58.6
Charleston, S.C	Sept. 4, 1938	ChM 38.207.5	3	23.9–45.2
33°15′ N., 76°23′ W	May 8, 1953	BLBG, *Gill* 2, Reg. 63	3	13.6–16.4
33°29′ N., 76°40′ W	Aug. 11, 1953	BLBG, *Gill* 3, Reg. 64	4	9.8–14.3
Magnolia Beach, S.C	September 1934	ChM 34.302.2	4	35.1–38.8
Do	October 1934	ChM 34.316.6	1	25.4
33°44′ N., 76°56′ W	Sept. 28, 1954	BLBG, *Gill* 8, Reg. 65	1	14.3
33°50′ N., 75°59′ W	July 10, 1954	BLBG, *Gill* 7, Reg. 72	1	18.6
34°04′ N., 76°14′ W	do	BLBG, *Gill* 7, Reg. 71	1	19.0
34°09′ N., 75°24′ W	Sept. 26, 1954	BLBG, *Gill* 8, Reg. 73	1	34.5
34°14′ N., 76°03 W	Sept. 15, 1959	BLBG, *Silver Bay*	2	14.7, 16.8
34°34′ N., 74°55′ W	Sept. 29, 1954	BLBG, *Gill* 8, Reg. 80	1	15.5
34°34′ N., 75°40′ W	July 24, 1960	BLBG, *Silver Bay* 2201	5	10.3–13.2
Off Cape Lookout, N.C	Sept. 2, 1914	USNM 111750, *Fish Hawk*	2	14.5, 17.3
Fort Macon Beach, Beaufort, N.C	July 27, 1916	USNM 111752	6	29.8–45.2
35°08′ N., 75°22′ W	Sept. 24, 1954	BLBG, *Gill* 8, Reg. 78	1	13.5
35°12′30″ N., 75°05′00″ W	Oct. 19, 1884	USNM 83846, *Albatross*	1	38.2
38°50′ N., 70°07′ W	Sept. 16, 1886	USNM 85501, *Albatross*	1	23.5
40°03′30″ N., 67°27′15″ W	July 15, 1885	USNM 133875, *Albatross*	2	30.8, 38.3
Woods Hole, Mass		USNM 58932	1	101.5
WESTERN NORTH ATLANTIC:				
Porto Inhuama, Brazil	May 1935	USNM 100812	1	233.0

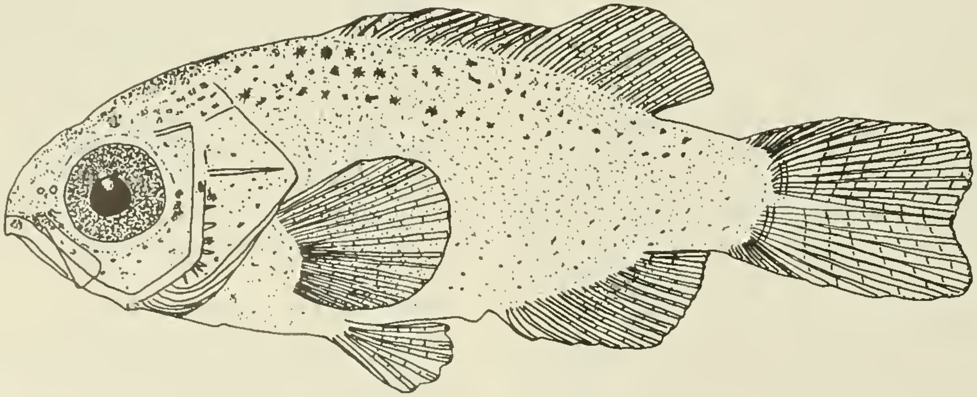

FIGURE 1.—*Kyphosus sectatrix* juvenile, 10.5 mm. (preserved for 7 years).

TABLE 3.—*Number of dorsal and anal soft-rays on 115 specimens of* Kyphosus sectatrix

Number of anal soft-rays	Number of dorsal soft-rays: 11	12	13
9	------	1 (0.9)	------
10	------	------	------
11	4 (3.5)	100 (86.9)	5 (4.3)
12	------	5 (4.3)	------

NOTE.—Open figures denote numbers; figures in parentheses denote percentages of specimens having respective combinations of numbers of soft-rays.

The last spine is pointed but still segmented, indicating near completion of a transition from a segmented ray to an unsegmented spine. Similar development has been noted in anal spines of mullet (Anderson, 1957) and striped bass (Mansueti, 1958). The transition completes the complement of the dorsal spines.

The spines are not inserted in a single mid-dorsal row, but rather alternately to the left and right of the mid-dorsal line. The interspinous membrane is nearly mid-dorsal in position, thus attaching to alternate sides of consecutive spines.

At 10.4 mm., all soft-rays are unbranched, except for the last which is divided to its base, all are segmented and the tips are all flattened. The next to last ray is branched by 13.1 mm., and by 15.4 mm., all but the first three soft-rays are branched (including both elements of the last). By 21.5 mm., all but the first soft-ray are branched, and by 26.4 mm., all soft-rays are branched.

Anal fin.—III (59 specimens) or IV (1 specimen)—9 (1 specimen), 11 (109 specimens), or 12 (5 specimens) (table 3). The full complement of rays is present by 10.4 mm., the soft-rays are segmented with tips flattened and the last ray is branched to its base (see fig. 1, 10.5 mm.). In an 8.7-mm. *K. incisor* the third ray is segmented and pointed, indicating a transition from segmented ray to unsegmented spine. Although I have no *K. sectatrix* that small, I expect the transition to occur in this species also. No additional soft-rays are branched by 13.2 mm. By 15.0 mm., the next to last and the anterior element of the last ray are branched (fig. 2), by 15.4 mm., 10 soft-rays are branched, and by 21.5 mm., all are branched. The first two spines articulate with the same bone in the only specimen having four anal spines.

Pectoral fin.—17 (8 specimens), 18 (77 specimens), or 19 (25 specimens) soft-rays (table 4). The full complement of rays is present by 10.4 mm. (see fig. 1, 10.5 mm.). In a 10.5-mm. cleared and stained specimen all but the first and last rays have flattened tips, all but the first and the last three rays are segmented, and all are unbranched. By 15.4 mm., initial branching has started in eight of the middle rays, and by 26.9 mm., all are segmented, and all but the first two and the last two are branched. By 52 mm., the first two rays and the last ray are still unbranched, though secondary branching has commenced in the 10 middle rays. The last ray is branched by 71.5 mm., but the first two rays remain unbranched to at least 260.0 mm., the largest specimen examined.

Pelvic fin.—I, 5 (53 specimens). Full complement of one spine and five soft-rays is present by 10.4 mm., with all five soft-rays segmented and the middle three branched (see fig. 1, 10.5 mm.). By 13.1 mm., the remaining soft-rays have also branched.

Caudal fin.—9+8 principal rays (50 specimens) and 9+9 secondary rays in a fully formed caudal fin. By 10.5 mm., all the principal rays are formed, with tips flattened (fig. 1), 8+8 secondary rays are present, and the two secondary rays adjacent to the principal rays in both dorsal and ventral lobes are segmented. By 13.1 mm., the principal rays have begun to branch, and by 15.0 mm. (fig. 2), branching is complete (the dorsalmost principal ray and ventralmost principal ray do not branch). The complement of secondary rays is complete (9+9) in a 15.4-mm.

TABLE 4.—*Number of pectoral fin-rays on 110 specimens of* Kyphosus sectatrix *and 71 specimens of* Kyphosus incisor

[Arranged by species and area of capture]

Species	Area of capture	Number of specimens with pectoral fin-rays numbering—			
		17	18	19	20
Kyphosus sectatrix.	Atlantic coast of United States	8	69	6	------
	Bermuda and northern Bahamas (including Antilles Current and excluding Florida Current).	------	3	16	------
	Caribbean Sea	------	4	2	------
	Eastern Atlantic	------	1	1	------
Kyphosus incisor.	Atlantic coast of United States	------	7	55	5
	Northern Bahamas (including Antilles Current and excluding Florida Current).	------	------	3	------
	Brazil	------	------	------	1

specimen. (The secondary rays were examined in cleared and stained material only.)

Gill rakers.—Entire first arch, 21 to 27; upper limb, 5 to 8; lower limb, 16 to 19; ceratobranchial bone, 11 to 14 (tables 5 and 6). The data indicate a very slight increase in number of gill rakers with increase in size from 10 to 260 mm. The number of rakers on the ceratobranchial bone increases slightly with growth, probably the result of migration of the first rakers from on, or by, the upper end of the basibranchial bone. In many specimens one raker is located virtually at the space between the two bones, and often the last one or two rakers on the ends of the upper or lower limbs are tubercles.

Scales.—Row above lateral line, 60 to 73; straight line, 47 to 64 (table 7). By 10.5 mm., the sides of the body and peduncle have scales, but the head, belly, and dorsal and anal fin bases are bare. By 15.4 mm., parts of the head have scales, the scales extend from the dorsal ends of the opercular flaps, forward to a perpendicular from the anterior edge of the pupil; there are patches of scales ventral and posteroventral to the orbit and on the upper part of the operculum; scales extend onto the bases of the middle principal rays of the caudal fin, and a small area forward of the pectorals and another small area under the proximal part of the pelvics are naked. By 26.4 mm., scales cover the bases of all fins and the head, except for the area around and anterior to the nostrils, the lips, the edge of the orbit, and the preopercular and opercular margins. Scales extend for about two-thirds of the length of the soft dorsal and anal fin rays by 52 mm., but extend out only about one-third on the pectoral and caudal and one-half on the separate rays of the pelvics. At 215.0 mm., the distal third of the pectoral is naked. All the fins have scales by 260.0 mm., except the dorsal and anal spines which have scales only at the bases and the pelvics which have scales only along the rays.

TABLE 5.—*Number of gill rakers on upper and lower limbs of first arch on 103 specimens of* Kyphosus sectatrix *larger than 16 mm.*

Number of upper-limb gill rakers	Number of lower-limb gill rakers: 16	17	18	19
5	------	2 (1.9)	1 (1.0)	------
6	3 (2.9)	40 (38.8)	25 (24.3)	1 (1.0)
7	------	7 (6.8)	20 (19.4)	3 (2.9)
8	------	------	------	1 (1.0)

NOTE.—Open figures denote numbers, and figures in parentheses denote percentages of specimens having respective combinations of numbers of gill rakers.

Teeth.—Dentition of the 10.5-, 15.4-, and the 36.2-mm. specimens was determined by clearing and staining.

A 10.5-mm. specimen had 10 uneven caniniform teeth in a row on each premaxillary, with a few villiform teeth behind this row, and six uneven caniniform teeth in a row on each dentary, all in various degrees of development.

On a 15.4-mm. specimen, there were 15 uneven caniniform teeth in a row on each premaxillary, five to nine uneven caniniform teeth on each dentary, with a few villiform teeth behind these on each jaw, and about two villiform teeth on each half of the vomer.

A 36.2-mm. specimen had 13 teeth in a row on each premaxillary, of which half were caniniform and half were incisor, and 12 teeth in a row on each dentary, also half of which were caniniform and half incisor. Other teeth were present behind the rows on the premaxillaries. The vomer and

TABLE 6.—*Variation in number of gill rakers on first arch of* Kyphosus sectatrix

[Specimens grouped by size]

Standard length	Number of specimens with gill rakers on first arch numbering—																	
	Entire arch							Upper limb				Lower limb				Ceratobranchial bone			
	21	22	23	24	25	26	27	5	6	7	8	16	17	18	19	11	12	13	14
10.5–15.9 mm	1	1	------	------	------	------	------	1	1	------	------	2	------	------	------	------	2	------	------
16.0–19.9 mm	------	1	2	------	------	------	------	1	2	------	------	------	3	------	------	------	1	1	------
20.0–29.9 mm	------	1	6	4	------	------	------	1	10	------	------	------	7	4	------	------	4	5	------
30.0–39.9 mm	------	1	15	10	2	------	------	------	24	4	------	1	18	8	1	------	13	14	------
40.0–49.9 mm	------	------	15	10	6	------	------	1	23	7	------	------	15	16	------	------	8	23	------
50.0–149.9 mm	------	2	------	5	3	2	------	------	5	7	------	2	2	6	2	1	1	10	------
150.0–260.0 mm	------	------	3	3	10	1	1	------	5	12	1	------	4	12	2	------	------	9	8

TABLE 7.—*Number of scales along straight line on 104 specimens of* Kyphosus sectatrix *and 54 specimens of* Kyphosus incisor *larger than 18 mm.*

[Arranged by species and area of capture]

Species	Area of capture	Number of specimens with scales along straight line numbering—																	
		47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64
Kyphosus sectatrix	Atlantic coast of United States	1	2	3	7	22	15	19	6	1	1				1				
	Bermuda and northern Bahamas (including Antilles Current and excluding Florida Current)										1	4		2	2	2	3	1	2
	Caribbean Sea								2	2	2		1						
	Eastern Atlantic										1						1		
Kyphosus incisor	Atlantic coast of United States								3	2	3	6	14	9	7	5	1		
	Northern Bahamas (including Antilles Current and excluding Florida Current)										1		1		1				
	Brazil												1						

tongue each had about 12 villiform teeth (6 on each side), and each pterygoid had about six teeth. The incisor teeth on the jaws had the horizontal base processes found in the adults. The rows of teeth were interspaced with both incisiform and caniniform types.

From about 100 mm., characteristic adult teeth are present. There are about 13 to 22 incisiform teeth in a row on each side of each jaw, with large horizontal basal processes as described by Jordan and Evermann (1898), Evermann and Marsh (1900), and Günther (1859). Villiform teeth are behind these rows. The patches of villiform teeth on the tongue and pterygoid are slightly larger than at smaller sizes, the vomer is still covered with teeth, and there are also some teeth on the palatines.

Pigmentation.—Unless otherwise noted the pigmentation described is on specimens preserved in formalin for 2 to 8 years (up to 55 mm.) and in alcohol for more than 20 years (above 55 mm.). This species has striped and spotted phases which Townsend (1929) found the fish could alternate quickly. Between 10 and 12 mm., small dark pigment spots cover most of the body and the fins, except for the caudal, the region of the first three dorsal and anal soft-rays, and the distal parts of the remainder of the soft dorsal and anal fins (fig. 1). There are larger, lighter brownish spots on the top of the head, upper lip, and before and behind the eye. Several rows of large dark spots are above the lateral line on some, or the dark spots may be more dense and uniform on the body on others. Also, some have faint brownish bands on the sides below the dorsal fin.

Between 12 and 15 mm., the first three dorsal and anal soft-rays have pigment spots, except at the tips (fig. 2). The intensity of pigment on the dorsal, anal, and pelvic fins is greater than on the smaller specimens.

Between 15 and 16 mm., the large brownish spots previously found on the head are absent. Small brownish spots extend along the scale rows and are most prominent above the lateral line. Small dark dashes are found along the pectoral rays. Dark pigment spots extend further out on the dorsal and anal soft-rays, and some spots are found in the middle of the caudal fin near the hypural base.

Between 18 and 19 mm., sides are brownish with light buff-colored patches (fig. 3A). The head is brownish dorsally and buff ventrally. The entire ventral surface back to the anal spine is buff.

Between 20 and 30 mm., the sides are generally buff with light brownish areas with dark stripes along scale rows above the lateral line. Usually the buff spots with brown background are more distinct than the dark stripes on preserved specimens (fig. 3B). Nearly all have pigment around the first three dorsal and anal soft-rays.

Between 30 and 75 mm., the whole body is dark with light patches (fig. 3C, D, and E), including the head, stomach, dorsal and anal fins, and the proximal half of the caudal fin. On specimens preserved about one year the same pattern is present, but the brown portion is gray and the dark parts are darker (fig. 3D).

Between 75 and 260 mm., there are no spots or light patches on the sides; brassy stripes follow along the scale rows of the specimens preserved for more than 20 years (fig. 3F). One 230-mm. specimen from Jamaica, preserved for less than one year, was slate gray on the sides.

Gray is given as the predominant color of adults in some accounts (Evermann and Marsh, 1900;

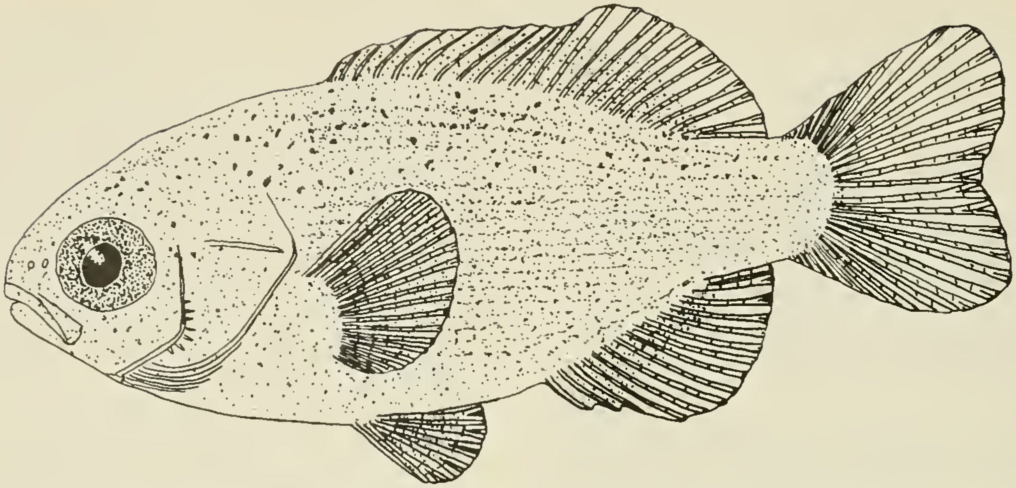

FIGURE 2.—*Kyphosus sectatrix* juvenile, 15.0 mm. (preserved for 7 years).

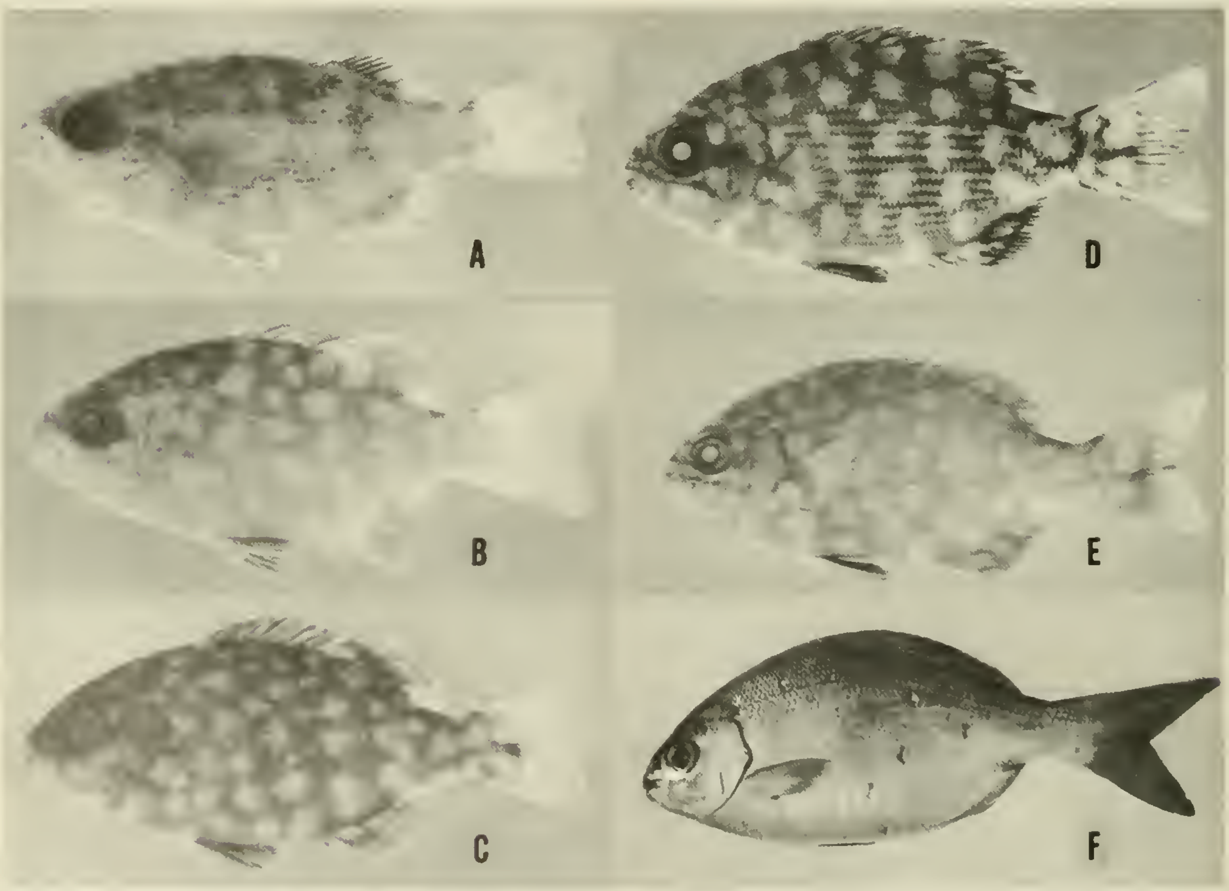

FIGURE 3.—*Kyphosus sectatrix;* A, juvenile, 18.7 mm. (preserved for 3 years); B, juvenile, 28.5 mm. (preserved for 7 years); C, juvenile, 33.3 mm. (preserved for 6 years); D, juvenile, 52.0 mm. (preserved for 1 year); E, juvenile, 71.5 mm. (preserved for 22 years); F, adult, 260.0 mm. (preserved for over 25 years).

and Truitt, Bean, and Fowler, 1929); Longley and Hildebrand (1941) do not mention gray in their description of this species.

DISTRIBUTION ALONG THE ATLANTIC COAST OF THE UNITED STATES AND THE NORTHERN BAHAMAS

Kyphosus sectatrix has previously been reported from the following specific localities in this area: Tortugas, Fla., by Jordan and Thompson (1905), and Longley and Hildebrand (1941); Key West, Fla., by Jordan (1884), Jordan and Fesler (1893), Evermann and Kendall (1900), and Fowler (1929; 1945); Card Sound opposite Key Largo, Fla., by Fowler (1945); Andros Island, Bahamas, by Rosen (1911); Fish Market at Nassau, Bahamas by Lee (1889); West Palm Beach, Fla., by Fowler (1929); Palm Beach, Fla., by Fowler (1915); East Coast of Fla., by Goode (1879); 31°13′ N. Lat., 74° W. Long., by Bean (1905); Charleston (pilot ship) and Magnolia Beach, S.C., by Fowler (1945); South Carolina, by Lacépède (1803); Beaufort Harbor, N.C., by Jordan and Gilbert (1879); Beaufort and Cape Lookout, N.C., by Smith (1907); Fisherman's Island, Va., by Hildebrand and Schroeder (1928); Worcester Co., Md., by Truitt, Bean, and Fowler (1929); Atlantic City, N.J., by Fowler (1952); Gravesend Bay, N.Y., by Bean (1897; 1903); Orient, N.Y., by Nichols and Breder (1927); Newport, R.I., by Kendall (1908) and Fowler (1917); and Woods Hole, Mass., by Baird (1873) and Smith (1898).

Some of these records may be of *Kyphosus incisor* since my study revealed that several others identified as *K. sectatrix* were actually *K. incisor*.

Figure 4 shows the location of capture of specimens examined from collections of cruises of the *Theodore N. Gill*, *Combat*, and *Silver Bay;* University of Florida specimen, Jupiter Inlet, Fla.; Charleston Museum specimens from Charleston and Magnolia Beach, S.C.; and U.S. National Museum specimens from the Bahamas, Angel Fish Creek, Fla., Broad Creek, Fla., and Beaufort, N.C.

Specimens of *K. sectatrix* taken from the following locations along the Atlantic coast of the United States are not shown in figure 4: Dry Tortugas, Fla., east of Delaware (38°25′ N., 72°40′ W.) and Woods Hole, Mass.

Except for some specimens from the Bahamas and Tortugas, all taken from the locations indicated (fig. 4) were juveniles, and most of these were taken under patches of *Sargassum*.

There is probably a northward drift in the Gulf Stream and Antilles Current of many of the developing young from adult populations in south Florida, the Bahamas, and the West Indies.

Most of the Bahama, Bermuda, and Antilles Current specimens I examined had higher scale and pectoral ray counts than the south Florida adults and most of the juveniles from other areas (tables 4 and 7). Most of the drifting juveniles caught north of south Florida and the Bahamas were probably from south Florida or another location not sampled. Since the specimens from the Caribbean Sea also had higher scale counts, though not as distinct, it is doubtful that many of the more northern juveniles came from there either. The specimen from Turks Island, described by Parr (1930) had a high scale count, as did the specimens I examined from the northern Bahamas.

The largest specimen from north of the Bahamas which I examined (133.0 mm., from Woods Hole, Mass.) approaches the size of the largest reported from the same region, about 6 inches (or about 150 mm.) by Smith (1898) at Woods Hole, Mass. There is no evidence that fully grown adults inhabit the Atlantic coast of the United States north of the Bahama Islands.

Table 8 shows the surface temperatures and salinities of the open waters along the Atlantic coast of the United States and the northern Bahamas at locations from which several juveniles were taken. Unfortunately, these data are not available for the specimens captured along the shoreline of the U.S. coast. Therefore, the indicated ranges of temperature, 23.61° C. to 29.02° C., and salinity, 35.39 °/oo to 36.53 °/oo, probably do not represent the ranges of tolerance for this

TABLE 8.—*Surface temperatures and salinities for times and locations of capture of 17 specimens of* Kyphosus sectatrix

[Data taken from the *Theodore N. Gill* cruise reports and unpublished station lists of the *Silver Bay*; specimens arranged individually by size]

Size mm.	Temperature °C.	Salinity °/oo	Date	Latitude and Longitude
10.5	28.41	36.27	Jan. 28, 1954	25°32′ N., 76°13′ W.
10.5	28.41	36.27	Oct. 8, 1953	24°28′ N., 77°28′ W.
10.5	28.41	36.27	do	24°28′ N., 77°28′ W.
11.3	28.16	36.12	Sept. 29, 1954	34°34′ N., 74°55′ W.
11.3	26.79	36.06	Apr. 27, 1954	29°00′ N., 79°48′ W.
12.0	24.30	36.53	Jan. 24, 1954	26°20′ N., 76°43′ W.
12.7	26.59	36.31	Sept. 28, 1954	33°44′ N., 76°56′ W.
13.1	27.80	35.39	Oct. 14, 1954	29°00′ N., 79°48′ W.
13.2	28.16	36.12	Sept. 29, 1954	34°34′ N., 74°55′ W.
15.0	28.07	35.91	Oct. 12, 1953	27°37′ N., 79°40′ W.
18.4	28.08	35.94	Oct. 14, 1953	29°36′ N., 79°58′ W.
26.4	24.20	36.52	Jan. 23, 1954	26°21′ N., 76°44′ W.
26.8	26.44	36.22	Oct. 26, 1953	32°18′ N., 77°29′ W.
28.5	26.40	36.29	Oct. 24–25, 1953	31°28′ N., 78°42′ W.
33.3	29.02	36.07	Sept. 13, 1954	29°40′ N., 80°00′ W.
34.7	27.75	36.47	June 13, 1954	26°23′ N., 76°46′ W.
52.0	23.61	----------	Oct. 26, 1959	32°15′ N., 79°14′ W.

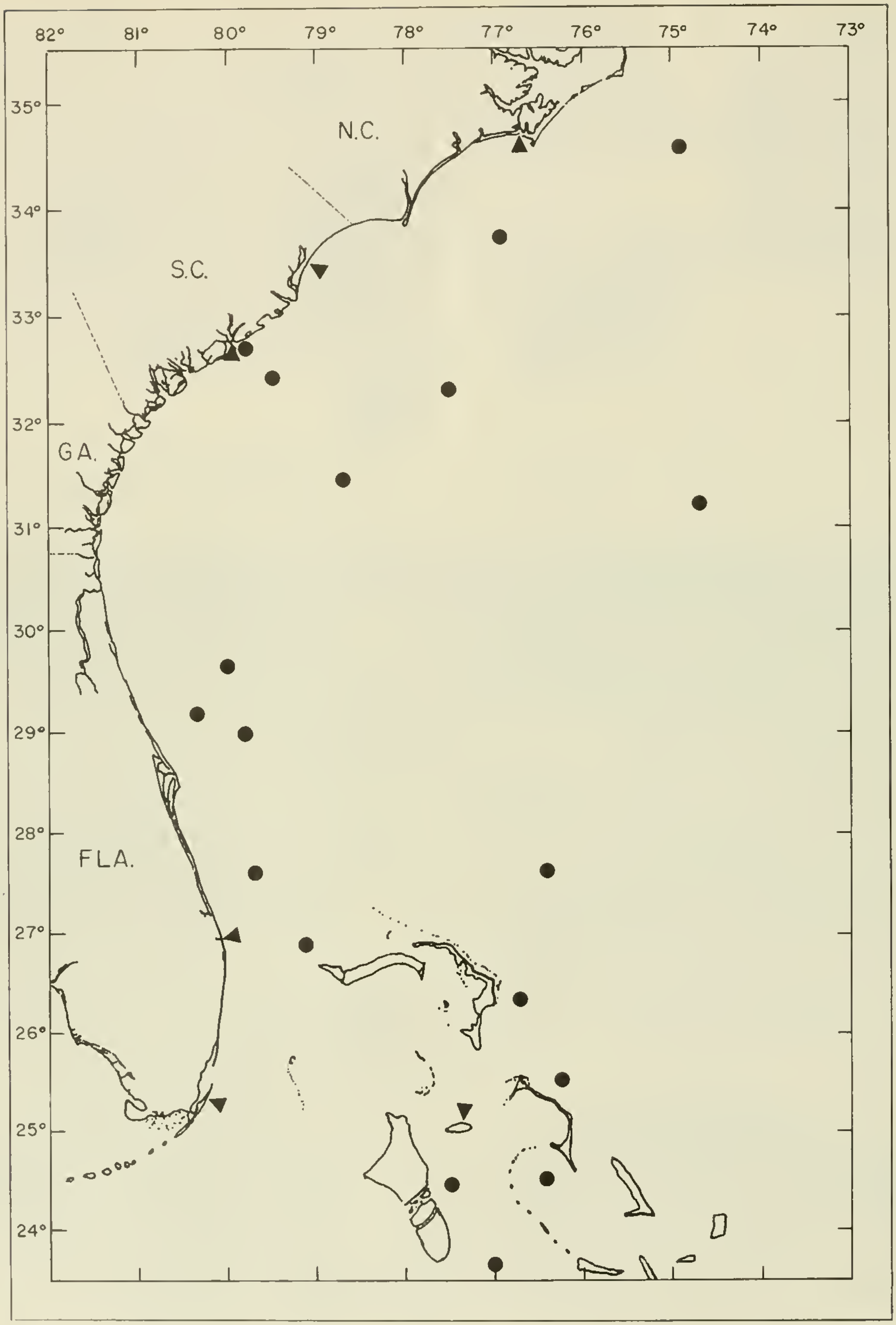

Figure 4.—Locations of capture of *Kyphosus sectatrix* along the southeastern Atlantic coast of the United States and the northern Bahamas. Triangles denote capture along shoreline, and dots denote capture in open water.

species but may represent the optimum ranges for developing juveniles. Bean (1897) reported this species to be hardy in the aquarium but unable to endure winter temperature.

At Woods Hole, Mass., in April, the month Smith (1898) reported this species, the highest daily surface water temperature taken over an 11-year period was 11.67° C. (U.S. Department of Commerce, 1955). At Montauk, N.Y., about 25 miles from Orient where Nichols and Breder (1927) reported this species taken on November 2, 1915, the highest November surface water temperature recorded during 8 years of sampling was 15.55° C. These records indicate a tolerance of these low temperatures for at least a short period. The scarcity of this species in fish collections made north of Cape Hatteras suggests *K. sectatrix* cannot endure low temperatures.

Size frequency data for small specimens show that specimens under 20 mm. were taken during several parts of the year (fig. 5). This possibly would indicate that spawning occurs over a wide period of time during the year, which is common among many fishes in tropical and semitropical

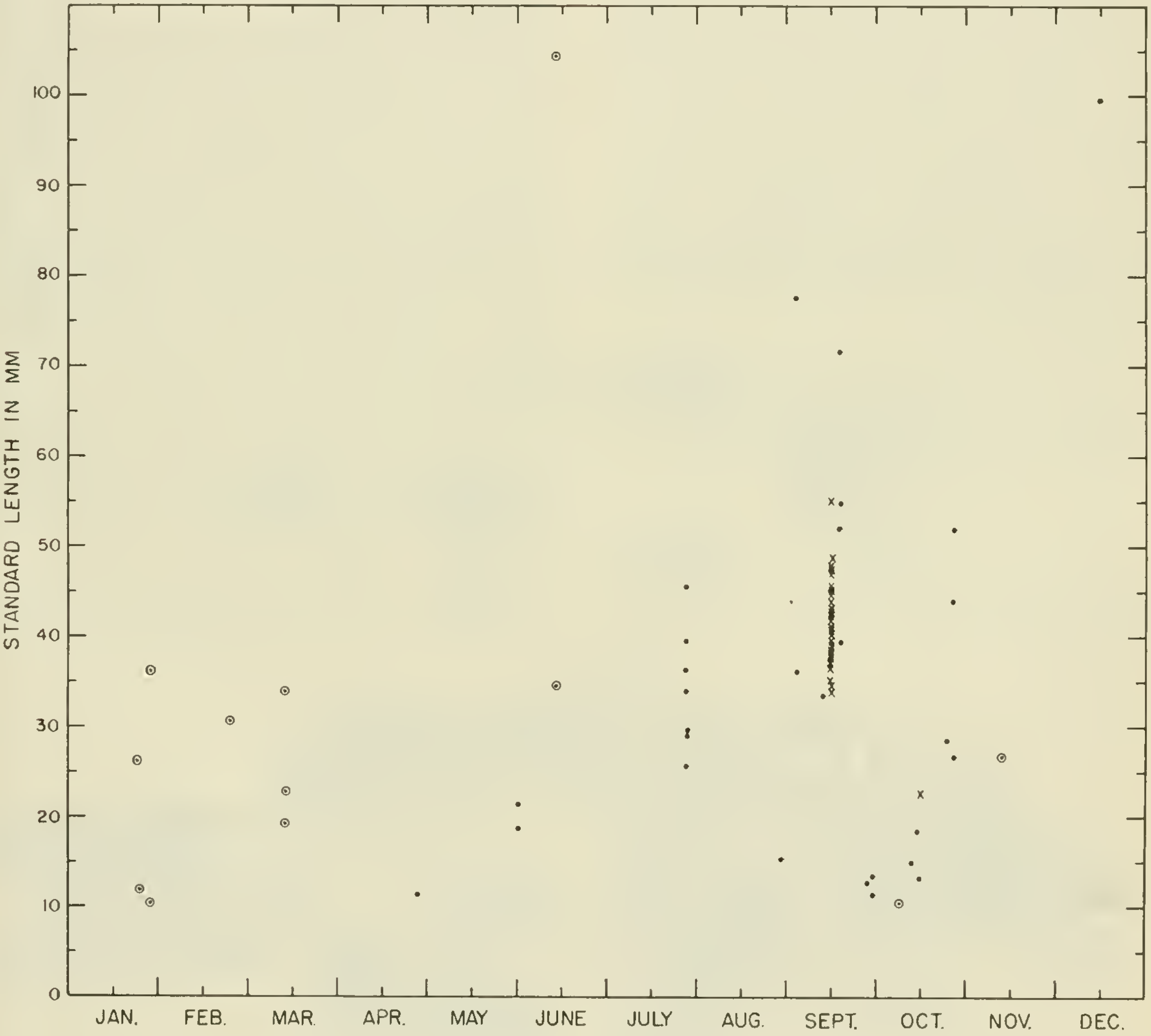

FIGURE 5.—Size distribution, by months, of 90 specimens of *Kyphosus sectatrix* taken along the Atlantic coast of the United States and the northern Bahamas. X's denote specimens having only month and year recorded in date of capture, and circles denote specimens captured in the northern Bahamas (including Antilles Current and excluding Florida Current).

waters. The sampling effort was not uniform throughout the seasons, therefore, many localities were not sampled during certain months.

Most of my specimens from the Bahamas and Antilles Current probably came from fall and winter spawning, and most from along the rest of the Atlantic coast of the United States probably came from spring and summer spawning.

KYPHOSUS INCISOR (CUVIER)

Pimelepterus incisor Cuvier in Cuvier and Valenciennes, 1831: p. 266 (Brazil).

Pimelepterus flavo-lineatus Poey, 1866: p. 319 (Havana).

The nomenclature of *Kyphosus incisor,* like *K. sectatrix,* has been decisive since Jordan and Gilbert (1883) brought widespread attention to the correct generic name, *Kyphosus* [Lacépède (1802) for *Kyphosus bigibbus*]. The authority given for *K. incisor* has varied among Cuvier and Valenciennes, Cuvier, and Parkinson. In his description Cuvier (Cuvier and Valenciennes, 1831) gave credit to Parkinson for having sketched and named this species *Chaetodon incisor;* however, he did not cite a previous paper.

The genus and species *Seleima aurata* Bowdich (1825) is listed in doubtful synonymy to *K. incisor* by Jordan, Evermann, and Clark (1930). The description by Bowdich (1825) for *Seleima aurata* is without doubt not a description of *Kyphosus.*

DEVELOPMENT

Dorsal fin.—IX (1 specimen), X (3 specimens), XI (61 specimens), or XII (1 specimen)—13 (33 specimens), 14 (65 specimens), or 15 (1 specimen) (table 9). Full complement of total dorsal rays (spines and soft-rays combined) is present by 8.5 mm. and the soft-rays are all segmented and unbranched except for the last which is divided to its base (fig. 6). Some specimens from 8.5 to 10.2 mm. long have the last spine pointed, but segmented, indicating near completion of the transition from segmented ray to unsegmented spine noted also in *K. sectatrix.* By 17.2 mm., the next to last ray has branched, and by 17.5 mm., all but the first two soft-rays and the posterior element of the last have branched. By 19.0 mm., only the first soft-ray remains unbranched; all have branched by 25.8 mm.

In this species the spines are inserted alternately to the left and right of the mid-dorsal line as in *K. sectatrix.* Two spines articulate to the same bone in the fin of the single specimen with 12 spines.

Anal fin.—III (66 specimens)—12 (17 specimens) or 13 (82 specimens) (table 9). The full complement of total anal rays (spines and soft-rays combined) is present by 8.5 mm. (fig. 6). One at 8.7 mm. has the third ray pointed but still segmented, indicating a transition from segmented ray to unsegmented spine as in the dorsal fin. From 8.5 to 17.2 mm., the soft-rays are all segmented and unbranched except for the last which is divided to its base. By 17.5 mm., all but the first two soft-rays and the posterior element of the last ray have branched. By 19.0 mm., only the first remains unbranched and it is branched by 21.7 mm.

Pectoral fin.—18 (7 specimens), 19 (58 specimens), or 20 (6 specimens) soft-rays (table 4). The

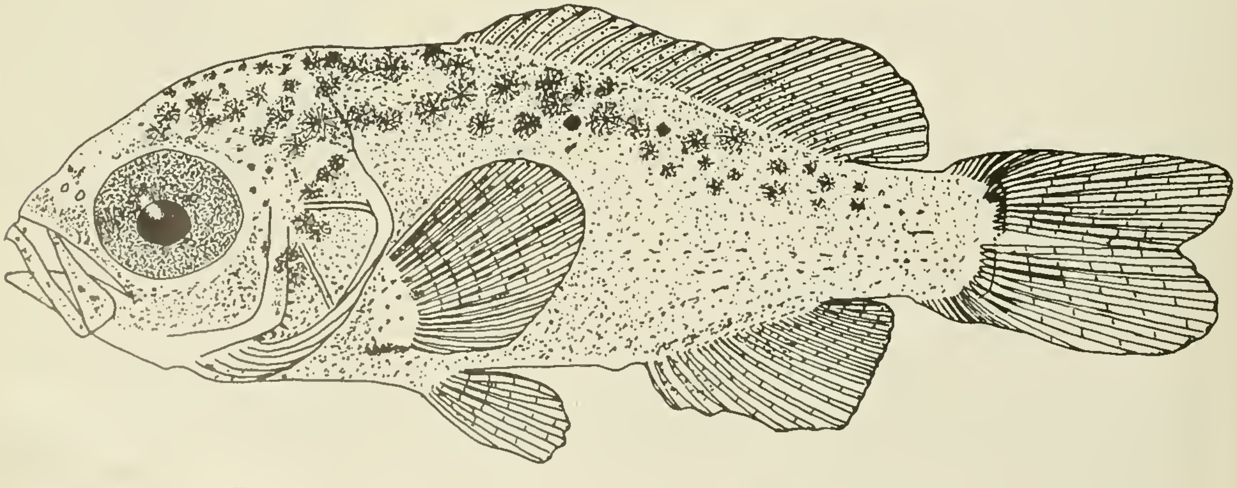

FIGURE 6.—*Kyphosus incisor* juvenile, 8.5 mm. (preserved for 2 years).

TABLE 9.—*Number of dorsal and anal soft-rays on 99 specimens of* Kyphosus incisor

		Number of dorsal soft-rays		
		13	14	15
Number of anal soft-rays	12	12 (12.1)	5 (5.0)	---- ----
	13	21 (21.2)	60 (60.6)	1 (1.0)

NOTE.—Open figures denote numbers; figures in parentheses denote percentages of specimens having respective combinations of numbers of soft-rays.

full complement of pectoral rays is present by 8.5 mm. The 2nd through 9th rays have flattened tips, and the 10th to the last have stout tapering tips (fig. 6). By about 10 mm., the 2nd through the last ray have flattened tips, and the 2nd through the 13th rays are segmented (fig. 7). At 15.8 mm., all rays are still unbranched, all but the first and last are segmented, and all but the first two and last one have flattened tips. By 28.4 mm., all the rays are segmented (one segment appearing in the first) and all but the first two and the last one are branched. At 50 mm., there has been no further branching. The last ray is branched by 58 mm., but the first two rays remain unbranched to 252 mm., the largest specimen examined.

Pelvic fin.—I, 5 (54 specimens). The full complement of pelvic rays is present by 8.5 mm. (fig. 6). All soft-rays are segmented but unbranched from 8.5 to 9.8 mm. (figs. 6 and 7). By 10 mm., the middle ray has branched, and by 13.6 mm., all soft-rays have branched.

Caudal fin.—9+8 principal rays (53 specimens) and 10+9 secondary rays in a fully formed caudal fin (the secondary rays were examined in cleared and stained specimens only). By 8.5 mm., all of the principal rays have formed, are segmented, and have flattened tips (fig. 6). A 10-mm. specimen had 9+8 secondary rays; the first on each lobe was an imbedded rudiment. By 11.4 mm., the secondary ray nearest the principals on the dorsal lobe is segmented. By 12.1 mm., the second ray from the principal rays on the ventral lobe is segmented. By 13.2 mm., the middle principal rays are just beginning to branch, and by 14.7 mm., the 12 middle principal rays have branched (fig. 8). A 15.8-mm., specimen had 10+8 secondary rays. By 16.1 mm., branching

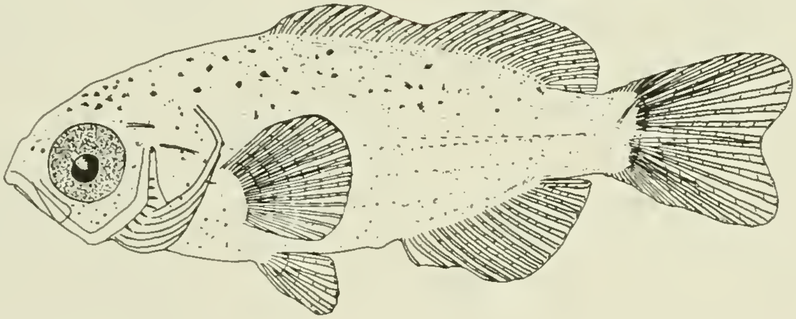

FIGURE 7.—*Kyphosus incisor* juvenile, 9.8 mm. (preserved for 7 years).

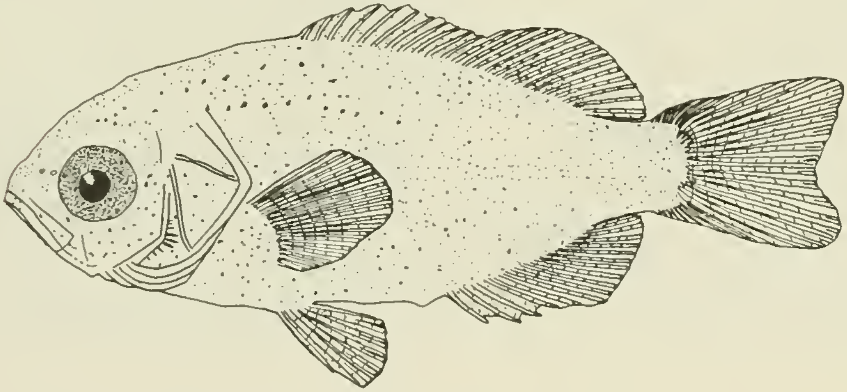

FIGURE 8.—*Kyphosus incisor* juvenile, 14.7 mm. (preserved for 7 years).

is complete (the principal ray nearest the secondaries on each lobe does not branch). By 19.2 mm., the two secondary rays adjacent to the principal rays, in both dorsal and ventral lobes, are segmented. A 28.4-mm. specimen had 10+9 secondary rays.

Gill rakers.—Entire first arch, 22 to 31; upper limb, 5 to 9; lower limb, 17 to 23; ceratobranchial bone, 13 to 15 (tables 10 and 11). The counts indicate a steady slow increase in number of gill rakers from 10 to 50 mm. with no increase beyond 50 mm.

Since this increase occurs in both limbs, the increase for the entire arch is more pronounced. The ceratobranchial-bone count, while showing the same trend, shows the least change; the change is probably the result of migration of the last raker, as in *K. sectatrix.*

Scales.—Row above lateral line, 63 to 73; straight line, 54 to 62 (table 7). By 8.5 mm., the sides are covered with scales from the pectoral base to the caudal peduncle and from just above the lateral line to the ventral edge of the pectoral base, with the same proportionate width back to the peduncle.

From 10 to 252 mm., the development of scales parallels that of *K. sectatrix.*

Teeth.—Dentition of the 10.0-, 15.8-, and 28.4-mm. specimens was determined by clearing and staining.

On a 10.0-mm. specimen, only premaxillary and dentary teeth were present; there were about 10 caniniform teeth in a row on each premaxillary and four on each dentary, all in various stages of development.

On a 15.8-mm. specimen, each premaxillary had 11 or 12 uneven caniniform teeth in a row, and each dentary had 4 or 5.

TABLE 10.—*Number of gill rakers on upper and lower limbs of first arch on 63 specimens of* Kyphosus incisor *larger than 16 mm.*

Number of upper-limb gill rakers	Number of lower-limb gill rakers: 19	20	21	22	23
6	6 (9.5)	6 (9.5)	--------	--------	--------
7	4 (6.3)	21 (33.3)	11 (17.5)	1 (1.6)	--------
8	--------	4 (6.3)	4 (6.3)	4 (6.3)	1 (1.6)
9	--------	--------	1 (1.6)	--------	--------

NOTE.—Open figures denote the numbers, and figures in parentheses, the percentages of specimens having respective combinations of numbers of gill rakers.

On a 28.4-mm. specimen, each premaxillary had 10 or 12 teeth in a row, half were caniniform and half were incisiform; and each dentary had 11 or 12 caniniform teeth in a row, with other teeth behind these rows on each jaw. The vomer had about 12 villiform teeth, each of 2 parallel patches on the posterior surface of the tongue had 6 villiform teeth, and the pterygoid had 2 villiform teeth in a tiny patch on the posterior surface.

From about 100 mm., the teeth resembled those of adult *K. sectatrix.*

Pigmentation.—By 8.5 mm., the smallest specimen examined, there are blotches of brownish-gray pigment with large blackish spots in the background and small black spots on the scales (fig. 6). The brownish-gray pigment extends over most of the spines and parts of the soft-dorsal and anal fins, but not over the area around the first three soft-rays of each fin. It also extends to the middle of the pelvic fins, with a few small black spots on these fins. On specimens about the same size, but preserved more than five years, the dark spots are distinct with no gray-brown pigment covering. The pectorals have some dark spots and stripes

TABLE 11.—*Variation in number of gill rakers on first arch of* Kyphosus incisor

[Specimens grouped by size]

Standard length	Number of specimens with gill rakers on first arch numbering—																								
	Entire arch										Upper limb					Lower limb							Cerato-branchial bone		
	22	23	24	25	26	27	28	29	30	31	5	6	7	8	9	17	18	19	20	21	22	23	13	14	15
8.5–15.9 mm	1	----	1	1	----	----	----	----	----	----	1	2	----	----	----	2	1	1	----	----	----	----	2	2	----
16.0–19.9 mm	----	----	----	3	2	1	1	----	----	----	----	5	2	----	----	----	----	3	3	1	----	----	----	4	----
20.0–29.9 mm	----	----	----	3	5	10	5	2	----	----	----	7	15	3	----	----	----	4	15	6	----	----	----	8	15
30.0–39.9 mm	----	----	----	----	3	6	4	2	----	1	----	----	14	2	----	----	----	3	5	6	1	1	1	6	9
40.0–49.9 mm	----	----	----	----	----	4	2	----	----	----	----	----	5	1	----	----	----	----	5	2	----	----	----	4	3
50.0–149.9 mm	----	----	----	----	----	----	1	1	2	----	----	----	1	3	----	----	----	----	1	1	2	----	----	----	4
150.0–252.0 mm	----	----	----	----	----	----	2	----	3	----	----	----	----	4	1	----	----	----	2	2	1	----	----	----	5

parallel and adjacent to the rays. The spots are present on the spinous-dorsal and anal fins and around the bases of the dorsal soft-rays. On the sides there are many pigment spots ranging from brown to black. Most of the larger spots have many narrow rays of pigment radiating out from each spot. The largest spots occur on the upper half of the side. The area over the gut cavity has spots larger than those on the rest of the lower half of the side, but smaller than those above. A straight line of black dashes under the surface lies on the middle of the side, at and just forward of the caudal peduncle; they are more visible on specimens preserved for an extended period of time (see fig. 7, 9.8 mm.).

By about 10 mm., the blotched gray pigment has become more distinct on the fresher specimens, however, the areas of pigment are about the same. The specimens, at this size, preserved for an extended time have slightly smaller dark spots than do the smaller fish (fig. 7).

On fresh specimens from about 11 to slightly longer than 13 mm., the gray pigment is more uniform (fig. 9A), which may be due to alternating color patterns like those found in *K. sectatrix* (Townsend, 1929). The pigment on the dorsal, anal, and pelvic fins is much darker than on most other parts. There still is no pigment on the caudal fin and little on the pectorals. The pigment on the soft dorsal ranges from none to some around the first three soft-rays. The preserved specimens of this size are similar to the fresh except that the gray is now brown. In the more faded condition, the dark spots are more pronounced than in the fresh condition, but not so distinct as in the smaller faded fish.

By about 15 mm., some specimens have pigment spots extending beyond the middle of the caudal

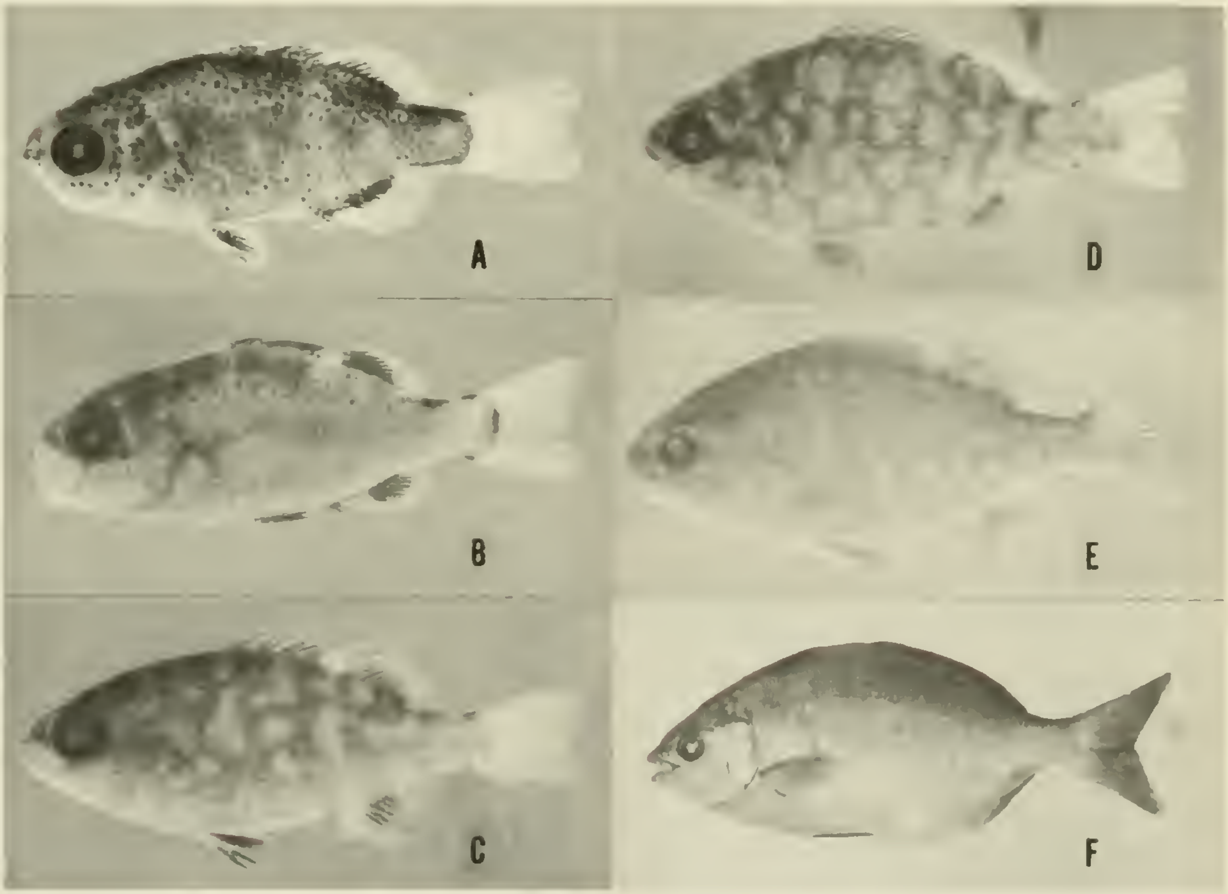

FIGURE 9.—*Kyphosus incisor;* A, juvenile, 13.2 mm. (preserved for 3 months); B, juvenile, 17.6 mm. (preserved for 2 years); C, juvenile, 21.2 mm. (preserved for 9 months); D, juvenile, 33.6 mm. (preserved for 3 years); E, juvenile, 54.5 mm. (preserved for 7 years); F, adult, 252.0 mm. (preserved for 74 years).

base (fig. 8). The fresher specimens show large patches of buff on brownish sides. Pigment spots extend further out on the soft dorsal and anal and cover most of the pectorals. In most fish through this size the first three soft-rays generally lack pigment.

From about 17 to 21 mm., the pigment covers more than half of the soft dorsal and anal fins. Extensive pigment over the anterior portions of these fins is more common than on the smaller specimens. There are light and dark streaks along the scale rows, and the patterns vary from light patches on dark background to a uniform slate gray, with the pigment on all but the pectoral fin being much darker (fig. 9B). By 21.2 mm., the pigment extends across the entire base of the caudal (fig. 9C).

From about 22 to 30 mm., there is a fine stippling of dark spots over most of the caudal and pectoral and the last two or three rays of the dorsal and anal. The stippling of the anterior third of the caudal is dense.

By 33.6 mm., the stippling on the fins is more dense (fig. 9D), even on very faded specimens. A darker band of pigment with black spots is becoming evident along the outer row of scales on the dorsal, anal, and caudal fins.

By 54.5 mm., the black band at the outer row of scales on the dorsal and anal fins has become more distinct (fig. 9E), and the dark spots on the sides of the fish are no longer apparent.

The larger specimens examined were old and had a uniform brassy appearance on the sides, with buff-tan on the underside (fig. 9F). The darker and lighter bands along the scale rows are apparent, and the fins have a more uniform dark buff color.

DISTRIBUTION ALONG ATLANTIC COAST OF THE UNITED STATES AND NORTHERN BAHAMAS

Kyphosus incisor has previously been reported from the following specific localities in this area: Tortugas, Fla., by Jordan and Thompson (1905) and Longley and Hildebrand (1941); and Nantucket, Mass., by Nichols and Breder (1927) who said, "the identification is open to question." The most northerly definite record of *K. incisor*, from off Cape Hatteras, N. C., is in the preliminary identification of the *Theodore N. Gill* cruise collection of specimens (Anderson and Gehringer, 1959b).

Figure 10 shows the location of capture of specimens examined from the collections of the *Gill*, *Combat*, and *Silver Bay*, and from St. Simons Island, Ga.; University of Florida specimens from Palm Beach and Jupiter Inlets, Fla.; Charleston Museum specimens from Charleston and Magnolia Beach, S.C.; and USNM specimens from Key West, Fla., Nassau, Bahamas, Beaufort, N.C., and Capes Lookout and Hatteras, N.C.

Specimens of *K. incisor* taken from the following locations along the Atlantic coast of the United States are not shown in figure 10: Tortugas, Fla.; east of Delaware (38°50′ N., 70°07′ W.); east of New Jersey (40°03′ N., 67°27′W.); and Woods Hole, Mass. Aside from the Woods Hole specimen (101.5 mm.), all from north of Nassau were less than 60 mm.; the only specimens longer than 150 mm. were from Nassau and the Tortugas.

These data give the following new inshore records for *K. incisor:* Key West, Fla.; Jupiter Inlet, Fla.; Palm Beach, Fla.; Nassau, Bahamas; St. Simons Island, Ga.; Charleston, S.C.; Magnolia Beach, S.C,; Beaufort, N.C.; and Woods Hole, Mass.; and new records far offshore east of Delaware and New Jersey. All specimens captured on cruises of the *Combat* and *Silver Bay* are from new locations. All of the Charleston Museum specimens from Charleston and Magnolia Beach, S.C., were identified as *K. sectatrix* by Fowler (1945), however, some are *K. incisor*.

Most juveniles were taken under patches of *Sargassum*, often along with *K. sectatrix*. The locations indicated in figure 10 suggest, even more distinctly, a northward drift in the Gulf Stream and Antilles Current than did the locations for *K. sectatrix*, especially off North Carolina.

Table 12 shows the surface temperatures and salinities of the waters from which several juveniles were taken. The extremes recorded were similar to those recorded for *K. sectatrix*, except for the lower extreme of salinity from a shoreline location (27.85 °/₀₀ at St. Simons Island, Ga.). The month of capture was not reported for the specimen from Woods Hole, Mass., but the highest surface temperature recorded there was 25.00° C. (U.S. Department of Commerce, 1955).

Size frequency data for small specimens indicate that spawning occurs during much of the year (fig. 11) as in *K. sectatrix*. All of the specimens less than 20 mm. were captured from May through December, suggesting that the spawning activity

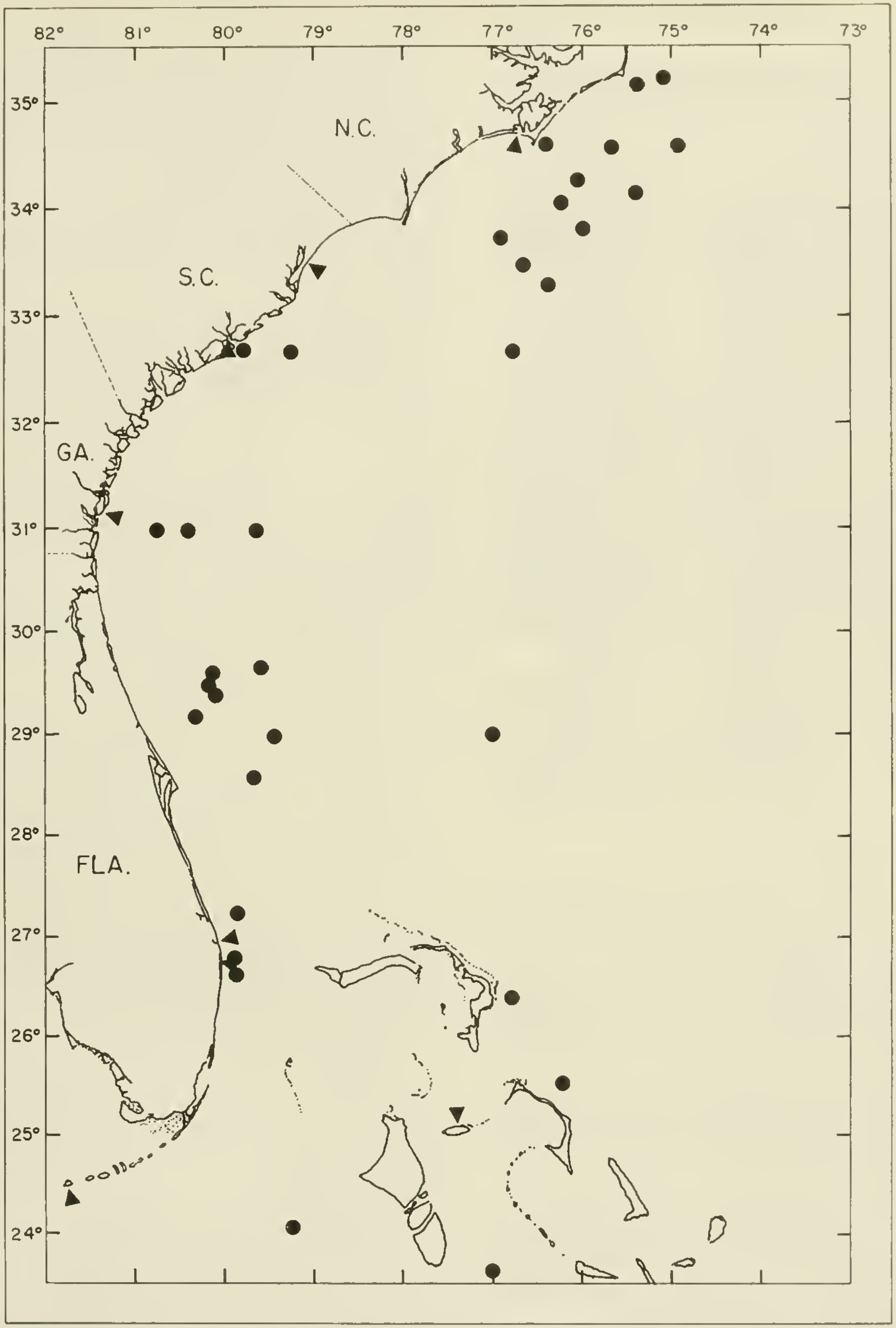

FIGURE 10.—Locations of capture of *Kyphosus incisor* along the southeastern Atlantic coast of the United States and the northern Bahamas. Triangles denote capture along shoreline, and dots denote capture in open water

TABLE 12.—*Surface temperatures and salinities for times and locations of capture of 41 specimens of* Kyphosus *incisor*

[Data from the *Theodore N. Gill* cruise reports, unpublished lists of the *Silver Bay*, and seining records of the Bureau of Commercial Fisheries Biological Laboratory, Brunswick, Ga., specimens arranged by size]

Size mm.	Temperature °C.	Salinity °/₀₀	Date	Latitude and longitude
8.7	27.94	36.04	Oct. 14, 1953	29°00′ N., 79°26′ W.
9.1	28.54	35.96	June 15, 1954	29°38′ N., 79°36′ W.
9.8	27.62	35.84	Aug. 11, 1953	33°29′ N., 76°40′ W.
10.0	28.54	35.96	June 25, 1954	29°38′ N., 79°36′ W.
10.3	28.89		July 24, 1960	34°34′ N., 75°40′ W.
11.4	28.89		do	Do.
11.9	28.89		do	Do.
12.1	27.62	35.84	Aug. 11, 1953	33°29′ N., 76°40′ W.
12.7	27.96	36.24	July 17, 1953	29°00′ N., 77°00′ W.
13.1	28.89		July 24, 1960	34°34′ N., 75°40′ W.
13.2	28.89		do	Do.
13.5	25.98	35.68	Sept. 24, 1954	35°08′ N., 75°22′ W.
13.6	25.04	36.36	May 8, 1953	33°15′ N., 76°23′ W.
13.7	25.04	36.36	do	Do.
14.2	27.62	35.84	Aug. 11, 1953	32°29′ N., 76°40′ W.
14.3	26.59	36.31	Sept. 28, 1954	33°44′ N., 76°56′ W.
14.3	27.62	35.84	Aug. 11, 1953	33°29′ N., 76°40′ W.
14.7	28.12	36.22	July 19, 1953	26°23′ N., 76°48′ W.
15.5	28.16	36.12	Sept. 29, 1954	34°34′ N., 74°55′ W.
16.2	28.81	36.02	Aug. 10, 1953	32°39′ N., 76°46′ W.
16.4	25.04	36.36	May 8, 1953	33°15′ N., 76°23′ W.
16.7	24.91	36.00	Oct. 16, 1953	31°00′ N., 80°23′ W.
17.2	27.51	36.55	June 13-14, 1954	26°20′ N., 76°47′ W.
18.2	[1] 27.85	[1] 36.15	Oct. 16, 1953	30°58′ N., 79°38′ W.
18.6	28.18	32.26	July 10, 1954	33°50′ N., 75°59′ W.
19.0	27.88	36.53	do	34°04′ N., 76°14′ W.
21.2	23.89		Jan. 28, 1960	29°36′ N., 80°08′ W.
23.4	23.89		Oct. 24, 1959	32°40′ N., 79°16′ W.
24.7	24.91	36.00	Oct. 16, 1953	31°00′ N., 80°23′ W.
25.4	23.89		Oct. 24, 1959	32°40′ N., 79°16′ W.
25.8	23.89		do	Do.
26.3	23.89		do	Do.
27.5	23.89		do	Do.
27.7	23.89		do	Do.
28.4	24.91	36.00	Oct. 16, 1953	31°00′ N., 80°23′ W.
28.6	23.89		Oct. 24, 1959	32°40′ N., 79°16′ W.
29.6	23.89		do	Do.
31.0	23.89		do	Do.
34.5	28.09	36.17	Sept. 9, 1954	34°09′ N., 75°24′ W.
37.5	24.25	35.37	Oct. 16, 1953	31°00′ N., 80°46′ W.
44.5	26.11	27.85	Oct. 5, 1955	St. Simons Island, Ga.

[1] Taken 10 meters below the surface.

is greatest during the spring and summer. It appears that the growth rate for juveniles may be as low as 10 mm. per month; however, my data were insufficient to establish the rate.

BODY PROPORTIONS OF *KYPHOSUS SECTATRIX* AND *KYPHOSUS INCISOR*

Eye diameter.—The relation of eye diameter to standard length indicates a very gradual decrease in rate of increase during growth, with no distinct inflections (fig. 12).

Eye diameter expressed as percentage of standard length ranged 11.2–16.5 percent from 8.5 to 30 mm., 10.4–13.4 percent from 30 to 60 mm., 8.3–12.0 percent from 60 to 150 mm., and 6.9–10.2 percent from 150 to 260 mm. (table 13).

Head length.—The relation of head length to standard length indicates a nearly constant rate of increase to about 50–60 mm. An inflection occurs at this size, with the rate of increase beyond 50–60 mm. constant but slightly lower than initially (fig. 13).

Head length expressed as percentage of standard length ranged 31.7–38.8 percent from 8.5 to 30 mm., 31.3–36.7 percent from 30 to 50 mm., 31.3–34.5 percent from 50 to 100 mm., and 25.5-32.0 percent from 100 to 260 mm. (table 13).

Body depth at pelvic fin.—The relation of body depth at pelvic fin to standard length shows a nearly constnt rate of increase through all sizes (fig. 14).

Body depth at pelvic fin expressed as percentage of standard length ranged 31.8-40.7 percent from 8.5 to 15 mm., 34.8–44.0 percent from 15 to 30 mm., and 38.4-47.7 percent from 30 to 260 mm. (table 13).

Snout to dorsal fin.—The relation of distance from snout to dorsal fin to standard length indicates a constant rate of increase through all sizes (fig. 15).

Distance from snout to dorsal fin expressed as percentage of standard length ranged 42.8–50.6 percent from 8.5 to 30 mm. and 38.8–47.5 percent from 30 to 260 mm. (table 13).

Snout to anal fin.—The relation of distance from snout to anal fin to standard length indicates a uniform rate of increase through all sizes (fig. 16).

Distance from snout to anal fin expressed as percentage of standard length ranged 60.8-68.4 percent from 8.5 to 20 mm. and 58.0-68.8 percent from 20 to 260 mm. (table 13).

Snout to pectoral fin.—The relation of distance from snout to pectoral fin to standard length shows an inflection in rate of increase at about 50-60 mm., with the rate beyond 50-60 mm. constant but lower than the initial rate (fig. 17).

Distance from snout to pectoral fin expressed as percentage of standard length ranged 31.3-40.0 percent from 8.5 to 20 mm., 28.7-36.8 percent from 20 to 60 mm., 26.6-31.2 percent from 60 to 140 mm., and 24.5-28.7 percent from 140 to 260 mm. (table 13).

Snout to pelvic fin.—The relation of distance from snout to pelvic fin to standard length shows a very gradual reduction in rate of increase from the smallest size to about 50-60 mm., after which the rate of increase appears constant and less than initially (fig. 18).

Distance from snout to pelvic fin expressed as percentage of standard length ranged 39.3-48.4

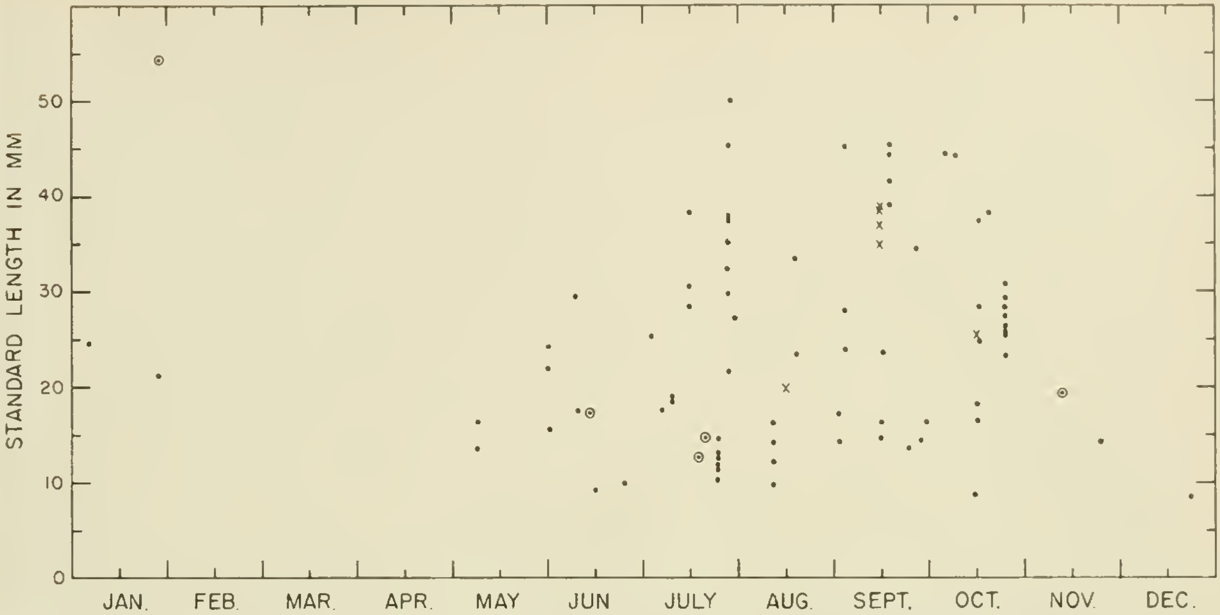

FIGURE 11.—Size distribution, by months, of 92 specimens of *Kyphosus incisor* taken along the Atlantic coast of the United States and the northern Bahamas. X's denote specimens having only month and year recorded in date of capture, and circles denote specimens captured in the northern Bahamas (including Antilles Current and excluding Florida Current).

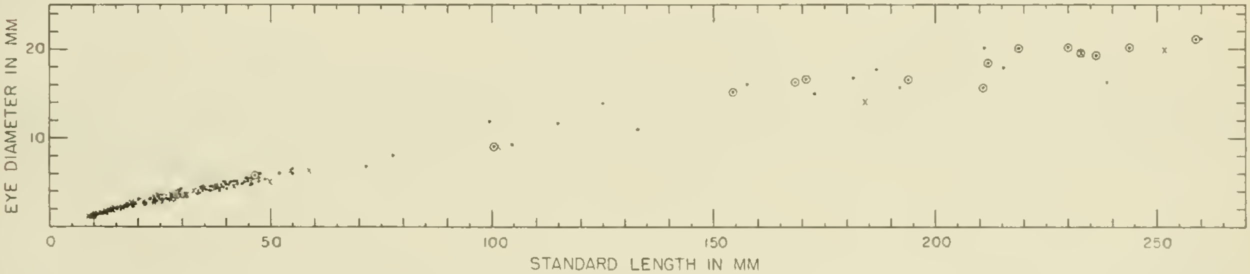

FIGURE 12.—Relation of eye diameter to standard length on 115 specimens of *Kyphosus sectatrix* and 99 specimens of *Kyphosus incisor*. Dots denote *K. sectatrix*, X's denote *K. incisor*, and circles denote capture beyond the Atlantic coast of the United States and the northern Bahamas.

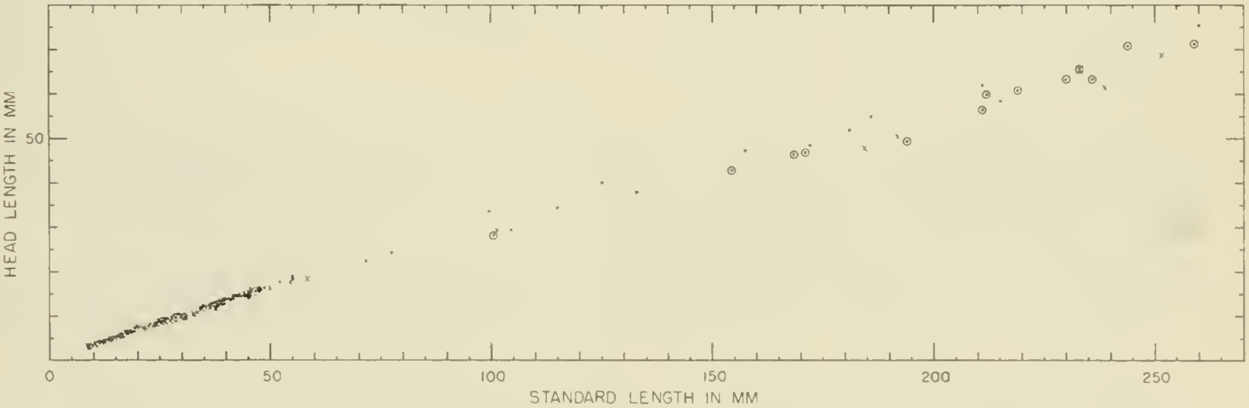

FIGURE 13.—Relation of head length to standard length on 115 specimens of *Kyphosus sectatrix* and 99 specimens of *Kyphosus incisor*. Dots denote *K. sectatrix*, X's denote *K. incisor*, and circles denote capture beyond the Atlantic coast of the United States and the northern Bahamas.

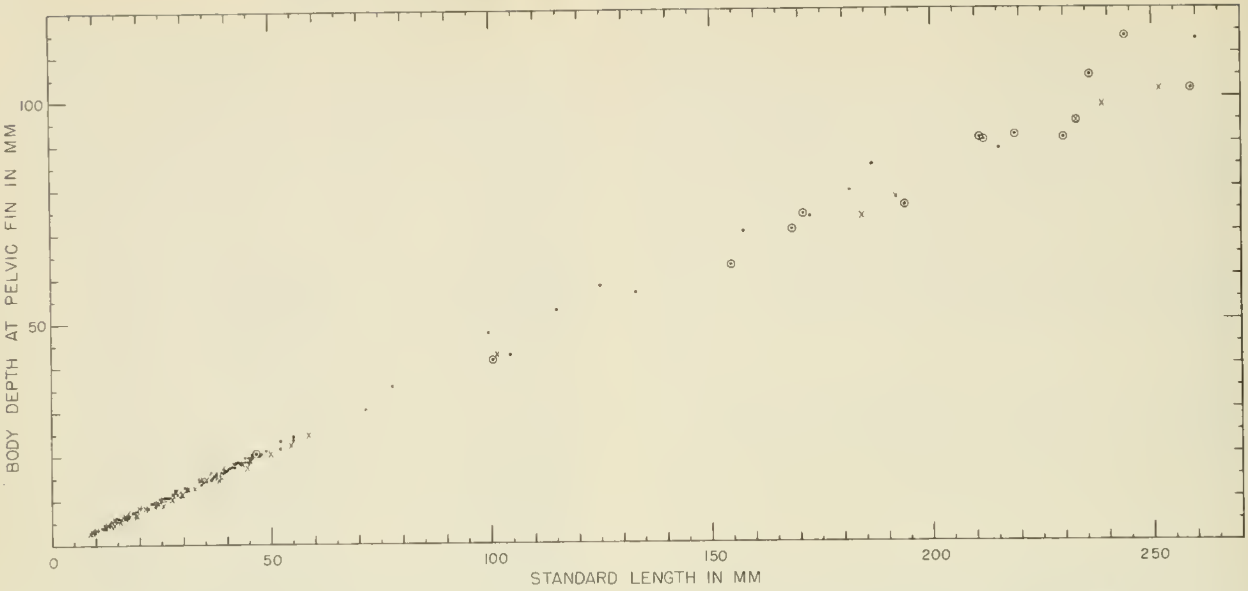

Figure 14.—Relation of body depth at pelvic fin to standard length on 115 specimens of *Kyphosus sectatrix* and 99 specimens of *Kyphosus incisor*. Dots denote *K. sectatrix*, X's denote *K. incisor*, and circles denote capture beyond the Atlantic coast of the United States and the northern Bahamas.

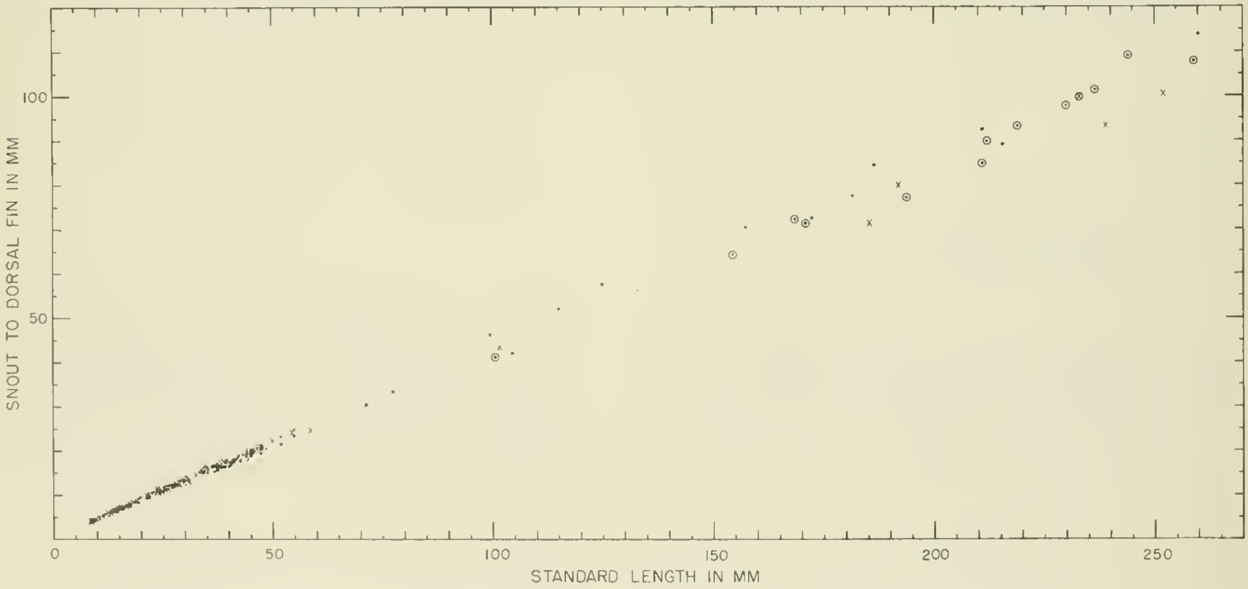

Figure 15.—Relation of distance snout-to-dorsal fin to standard length on 115 specimens of *Kyphosus sectatrix* and 97 specimens of *Kyphosus incisor*. Dots denote *K. sectatrix*, X's denote *K. incisor*, and circles denote capture beyond the Atlantic coast of the United States and the northern Bahamas.

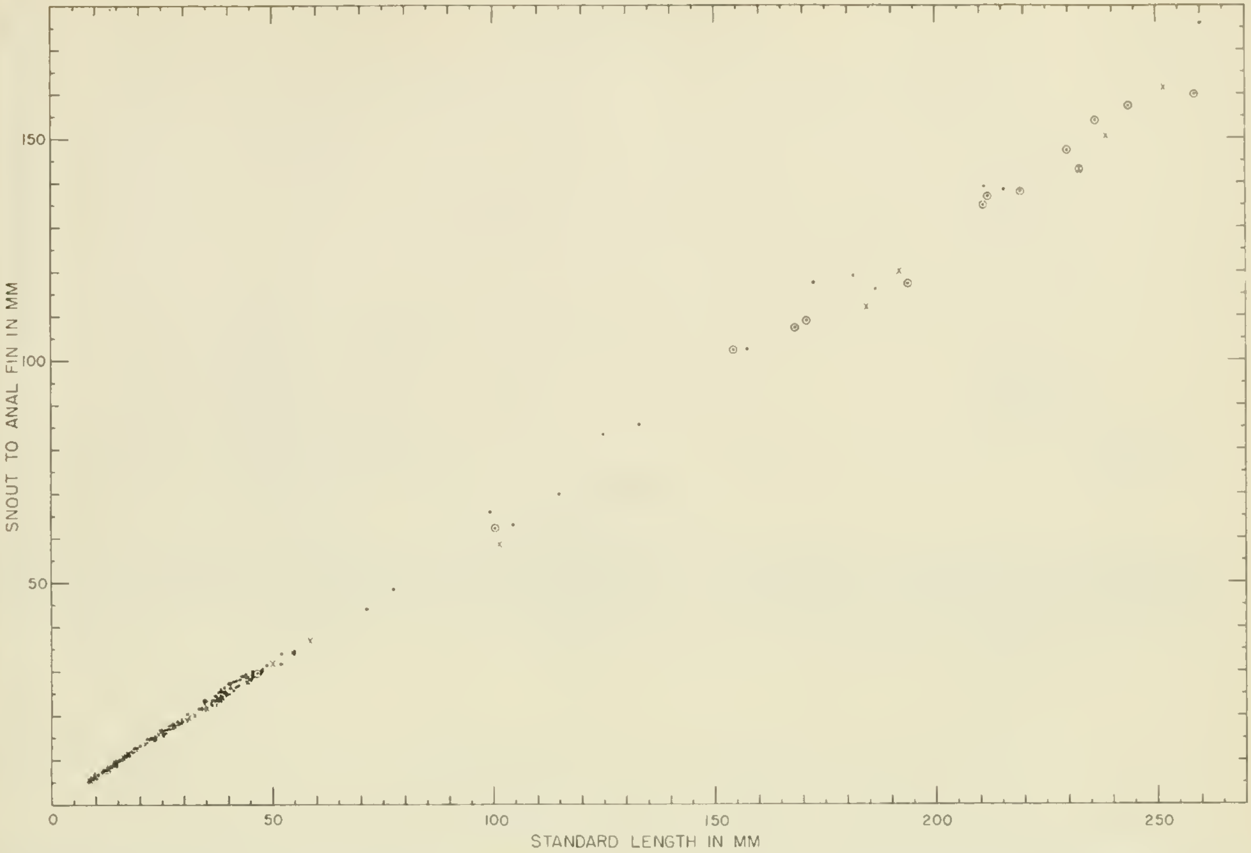

FIGURE 16.—Relation of distance snout-to-anal fin to standard length on 115 specimens of *Kyphosus sectatrix* and 98 specimens of *Kyphosus incisor*. Dots denote *K. sectatrix*, X's denote *K. incisor*, and circles denote capture beyond the Atlantic coast of the United States and the northern Bahamas.

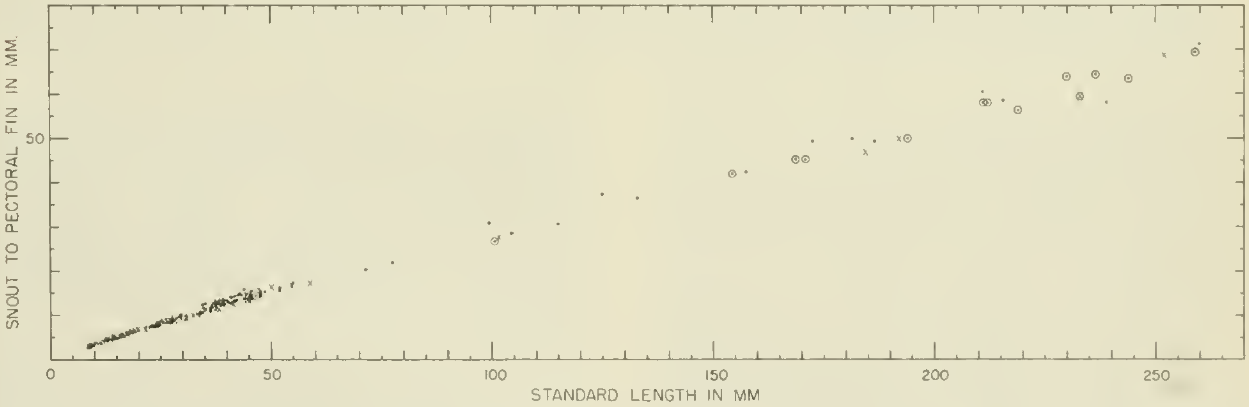

FIGURE 17.—Relation of distance snout-to-pectoral fin to standard length on 115 specimens of *Kyphosus sectatrix* and 99 specimens of *Kyphosus incisor*. Dots denote *K. sectatrix*, X's denote *K. incisor*, and circles denote capture beyond the Atlantic coast of the United States and the northern Bahamas.

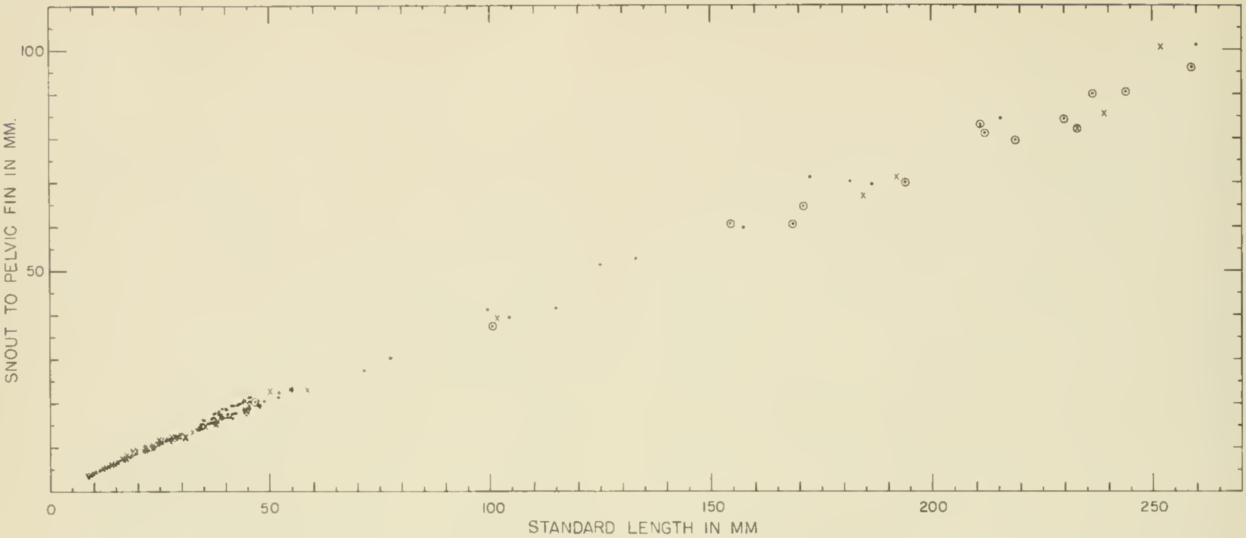

FIGURE 18.—Relation of distance snout-to-pelvic fin to standard length on 115 specimens of *Kyphosus sectatrix* and 99 specimens of *Kyphosus incisor*. Dots denote *K. sectatrix*, X's denote *K. incisor*, and circles denote capture beyond the Atlantic coast of the United States and the northern Bahamas.

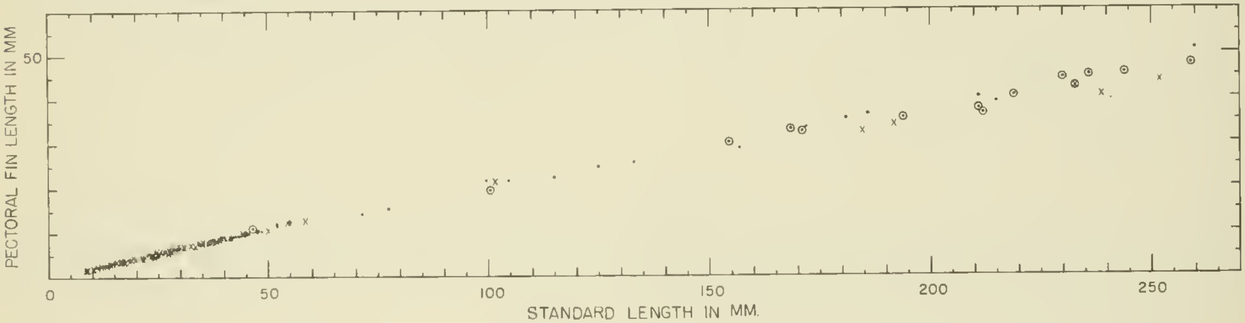

FIGURE 19.—Relation of pectoral fin length to standard length on 100 specimens of *Kyphosus sectatrix* and 94 specimens of *Kyphosus incisor*. Dots denote *K. sectatrix*, X's denote *K. incisor*, and circles denote capture beyond the Atlantic coast of the United States and the northern Bahamas.

percent from 8.5 to 60 mm. and 35.2-41.2 percent from 60 to 260 mm. (table 13).

Pectoral fin length.—The relation of pectoral fin length to standard length shows a uniform rate of increase to about 50-60 mm., with the rate beyond 60 mm. relatively uniform but lower than initially (fig. 19).

Pectoral fin length expressed as percentage of standard length ranged 18.9-24.1 percent from 8.5 to 20 mm., 19.4-24.1 percent from 20 to 60 mm., and 16.9-21.9 percent from 60 to 260 mm. (table 13).

COMPARISON OF THE SPECIES

ANATOMY AND APPEARANCE

Dorsal fin.—No interspecific variation in number of dorsal spines was observed, as more than four-fifths of the specimens of each species had 11 spines. Number of dorsal soft-rays is one of the best characters for separating *K. sectatrix* from *K. incisor* (fig. 20). In *K. sectatrix* 91 percent had 12 rays; in *K. incisor* 99 percent had 13 or 14 rays. Soft-rays start branching by 13.1 mm. in *K. sectatrix*, but not before 17.2 mm. in *K. incisor*.

Anal fin.—No interspecific variation in number of anal spines was observed. Number of anal soft-rays is another good character for separating *K. sectatrix* from *K. incisor* (fig. 20). In *K. sectatrix* 95 percent had 11 rays; in *K. incisor* 100 percent had 12 or 13 rays. Soft-rays start branching by 15.0 mm. in *K. sectatrix*, but not before 17.5 mm. in *K. incisor*.

Pectoral fin.—Interspecific variation in number of pectoral rays was indistinct throughout the

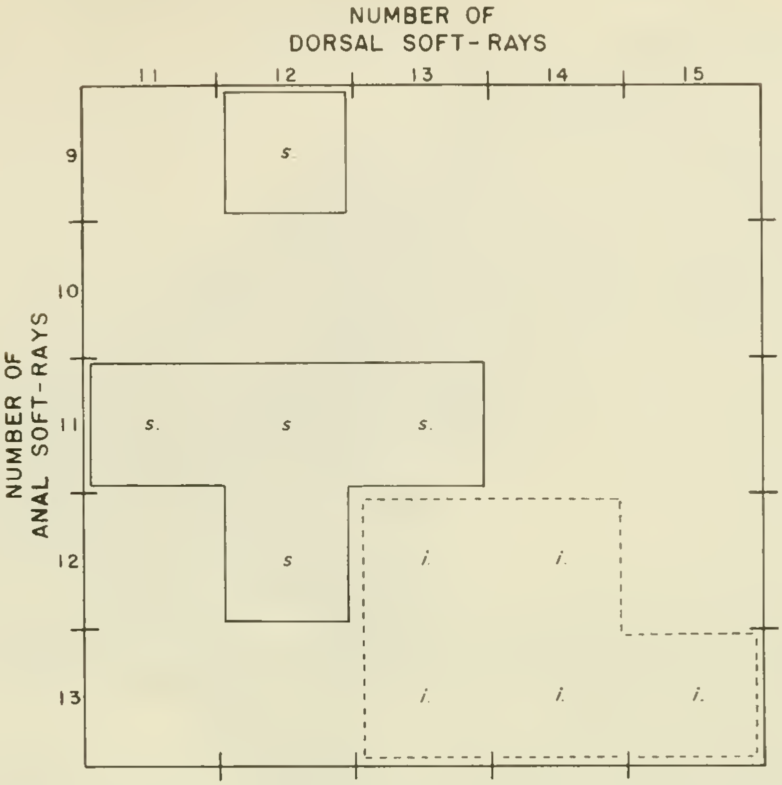

FIGURE 20.—Comparison of number of dorsal and anal soft-rays on 214 specimens of *Kyphosus* from the North Atlantic Ocean. Solid lines, enclosing *s.*'s, denote *K. sectatrix;* dashed lines, enclosing *i.*'s, denote *K. incisor.*

geographical ranges of both species, but distinct within much of the region intensively studied. In *K. sectatrix* 70 percent had 18 rays, 23 percent had 19 rays; in *K. incisor* 82 percent had 19 rays. Eighty-four percent of the specimens of *K. sectatrix* taken at Bermuda, the Bahamas, and in the Antilles Current had 19 rays, the normal count for *K. incisor;* 83 percent of those taken along the Atlantic coast of the United States had 18 rays (table 4). This indicates a population of *K. sectatrix,* in the Bahama-Bermuda region, distinct from the population found along the Atlantic coast of the United States. Soft-rays start branching in *K. sectatrix* by 15.4 mm. (in 8 rays); in *K. incisor* branching begins after 15.8 mm.

Pelvic fin.—No interspecific or intraspecific variations in the pelvic fin were observed.

Caudal fin.—No interspecific or intraspecific variations were observed in the principal caudal rays. In the dorsal lobe of the caudal fin, two *K. sectatrix* longer than 15 mm. had 9 secondary rays; two *K. incisor* more than 15 mm. had 10 secondary rays. Since secondary rays were counted only on six cleared and stained specimens (4 longer than 15 mm.), the value of this character for distinguishing the two species is questionable.

Gill rakers.—Numbers of first-arch gill rakers were good characters for separating *K. sectatrix* from *K. incisor* (fig. 21). On the entire first arch of specimens more than 16 mm., 96 percent of the *K. sectatrix* had 22 to 25 gill rakers, while 90 percent of the *K. incisor* had 26 to 31 gill rakers. On the upper limb of first arch of specimens above 16 mm., 67 percent of the *K. sectatrix* had 6 gill rakers, and 29 percent had 7 gill rakers; 19 percent of the *K. incisor* had 6 gill rakers and 80 percent had 7 or 8 gill rakers. On the lower limb of first arch of specimens above 16 mm., 92 percent of the *K. sectatrix* had 17 or 18 gill rakers; 75 percent of the *K. incisor* had 20 or 21 gill rakers. On the ceratobranchial bone, including all sizes, 91 percent of the *K. sectatrix* had 12 or 13 gill rakers; 95 percent of the *K. incisor* had 14 or 15 gill rakers.

Scales.—Interspecific variation in number of scales was indistinct throughout the geographical ranges of both species, but distinct within much

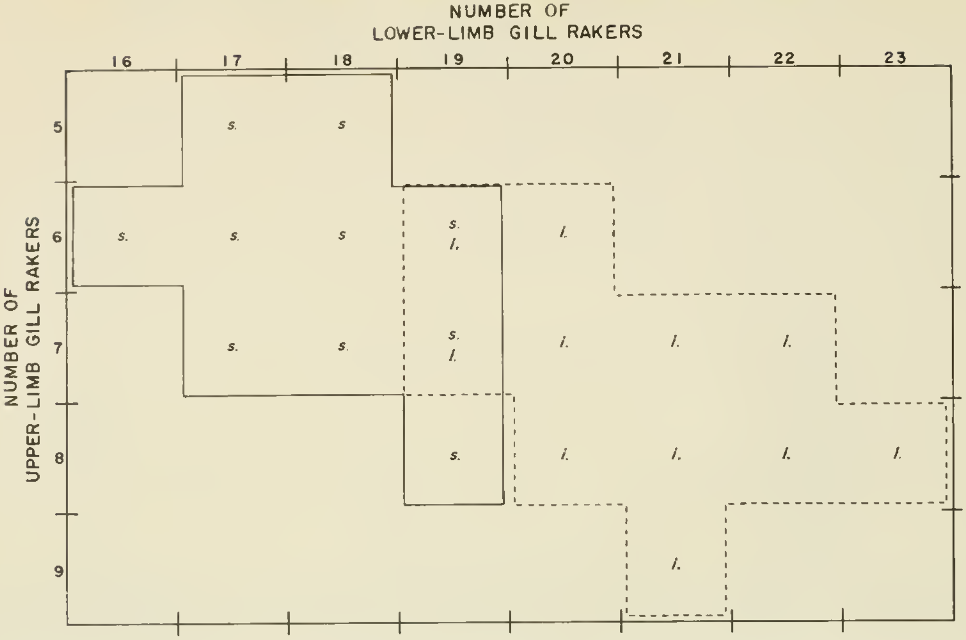

FIGURE 21.—Comparison of number of upper-limb and lower-limb gill rakers on the first arch of 165 specimens of *Kyphosus*, larger than 16 mm., from the North Atlantic Ocean. Solid lines, enclosing *s.*'s, denote *K. sectatrix;* dashed lines, enclosing *i.*'s, denote *K. incisor.*

of the region intensively studied. All specimens of *K. sectatrix* taken at Bermuda, the Bahamas, and in the Antilles Current had about the same number of scales (56 to 64), *K. incisor* has (54 to 62), counted in a straight line. All but one *K. sectatrix* taken along the Atlantic coast of the United States fell within a lower range (47 to 56) (table 7). The seven *K. sectatrix* taken in the Caribbean Sea had intermediate scale counts (54 to 58). As with pectoral fin rays, the straight-line scale counts indicate a distinct population of *K. sectatrix* in the Bahama-Bermuda region.

Teeth.—No interspecific variation in number of teeth on the premaxillary and dentary bones was observed.

Pigmentation.—The color patterns observed indicate that the ability to change pattern quickly, from bars to patches, observed by Townsend (1929) in *K. sectatrix,* is equally present in *K. incisor.* No comparison was made of fresh adult specimens. During development the color patterns are similar, except that most *K. incisor* from about 12 to 22 mm. have few or no pigment spots in the area of the first three dorsal and anal soft-rays, and few dark spots and lines on the pectorals (figs. 8, 9 A, B, and C); most *K. sectatrix* longer than 12 mm. have much heavier pigment on these parts (figs. 2 and 3A).

Caudal osteology.—No interspecific or intraspecific variations in caudal osteology were observed. A representative caudal base is illustrated in figure 22.

Branchiostegals.—Both species normally have seven branchiostegals on each side. However, one specimen of *K. incisor* had eight on one side and in this instance the first two were much closer together.

BODY PROPORTIONS

A slight indication of interspecific variation in eye diameter appeared only among specimens above 150 mm. (fig. 12). The eye diameters of all 18 *K. sectatrix* more than 150 mm. were 8.2 percent or more of standard length, except one specimen from Madeira (7.5 percent); those of the five *K. incisor* above 150 mm. long were 8.4 percent or less of standard length (table 13).

An indication of interspecific variation in head length, body depth at pelvic fin, and pectoral fin length appeared only among specimens more than 150 mm. from along the Atlantic coast of the

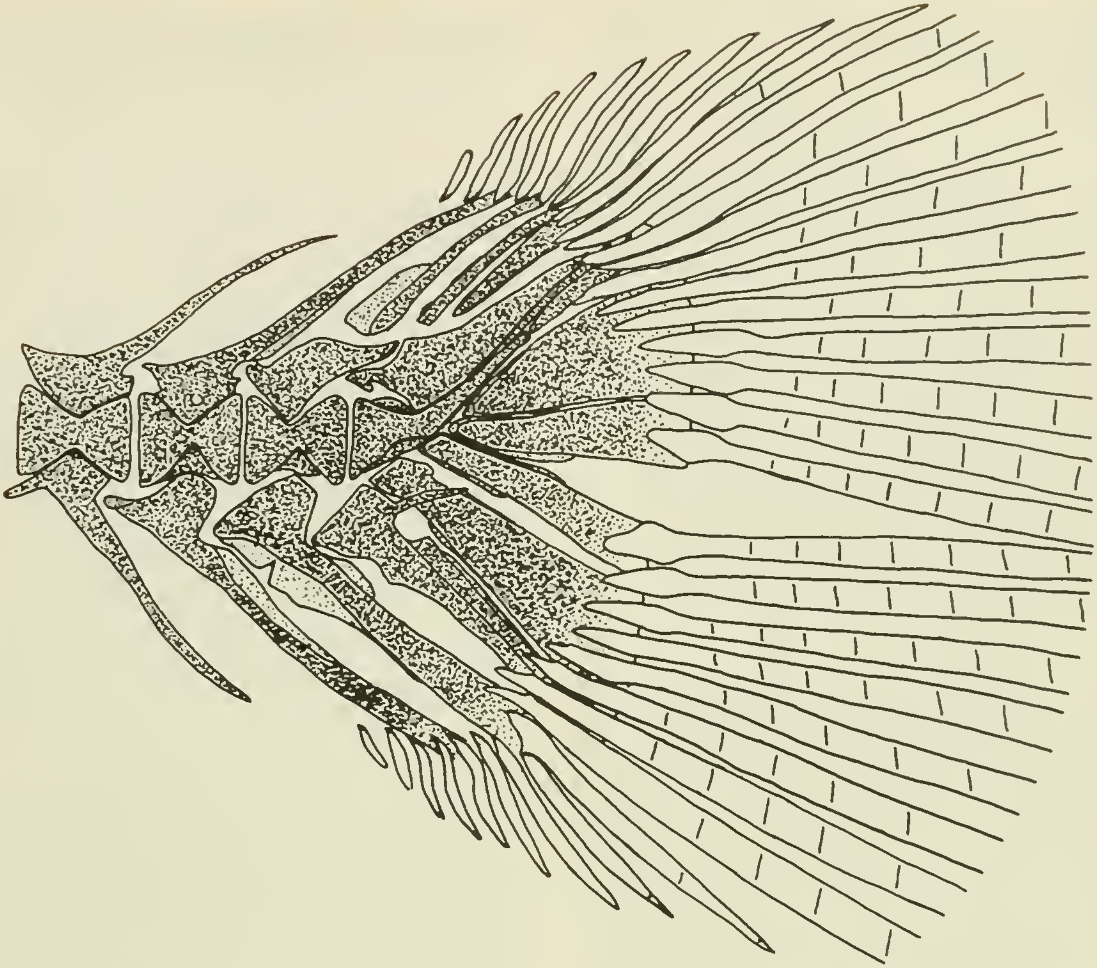

FIGURE 22.—Caudal skeleton of a 28.4-mm. *Kyphosus incisor*. (Camera lucida drawing from a cleared and stained specimen.)

United States and the northern Bahamas (figs. 13, 14, and 19). The three body proportions of these specimens, seven *K. sectatrix* and four *K. incisor*, expressed as percentage of standard length, showed the following: the head lengths of *K. sectatrix* were more than 27 percent, while those of *K. incisor* were less than 27.5 percent; the body depths at pelvic fin of *K. sectatrix* were 41 percent or more, while those of *K. incisor* were 41 percent or less; and the pectoral fin lengths of *K. sectatrix* were above 18 percent, while those of *K. incisor* were less than 18 percent (table 13).

There was little or no indication, at any size, of interspecific variation in the distances from snout to dorsal, anal, pectoral, and pelvic fins (figs. 15, 16, 17, and 18).

TABLE 13.—*Measurements of selected body parts of 115 specimens of* Kyphosus sectatrix *and 99 specimens of* Kyphosus incisor, *expressed as percentage of standard length*

KYPHOSUS SECTATRIX

Standard length (mm.)	Percent of standard length							
	Eye diameter	Head length	Depth at pelvic fin	Snout to dorsal fin	Snout to anal fin	Snout to pectoral fin	Snout to pelvic fin	Pectoral fin length
10.4 [1]	13.3	36.2	35.5	49.0	65.4	35.5	42.9	22.6
10.5 [1]	14.9	38.3	34.6	47.6	65.7	34.6	44.8	23.0
10.5 [1]	14.2	37.8	35.1	48.6	61.9	34.0	43.0	21.5
11.3	14.0	35.6	34.8	46.9	65.5	32.7	41.6	22.2
11.3	13.4	36.9	35.8	48.7	65.5	34.8	42.7	21.4
12.0 [1]	13.5	34.8	39.2	49.2	65.0	34.2	43.2	24.1
12.7	13.9	36.1	35.6	48.0	61.4	34.6	40.9	23.1
13.1	14.6	37.1	35.4	49.6	66.4	34.5	44.3	20.9
13.2	13.9	35.4	38.6	47.0	62.9	32.4	42.4	22.2
15.0	14.4	35.3	40.7	46.7	65.3	32.1	42.7	21.0
15.4	13.9	36.4	39.0	44.8	66.2	31.3	41.6	22.4

See footnotes at end of table.

TABLE 13.—*Measurements of selected body parts of 115 specimens of* Kyphosus sectatrix *and 99 specimens of* Kyphosus incisor, *expressed as percentage of standard length*—Continued

KYPHOSUS SECTATRIX—Continued

Standard length (mm.)	Percent of standard length							
	Eye diameter	Head length	Depth at pelvic fin	Snout to dorsal fin	Snout to anal fin	Snout to pectoral fin	Snout to pelvic fin	Pectoral fin length
18.4	14.9	36.4	39.7	46.2	64.1	32.6	41.8	22.3
18.7	12.1	34.2	39.0	44.4	68.4	32.1	45.5	20.4
19.4 [1]	13.4	34.0	40.2	47.4	66.0	32.0	42.3	23.7
20.0 [1]	15.5	36.5	42.5	48.0	66.0	32.0	43.5	-------
21.5	12.3	34.0	38.6	42.8	68.8	33.5	47.4	21.3
22.5	13.8	35.1	43.1	47.6	65.8	32.0	41.3	22.7
22.9 [1]	14.4	35.8	41.9	47.2	65.5	33.6	44.1	24.0
25.6	14.5	37.9	41.8	47.7	66.0	32.4	43.0	23.0
26.1	12.6	37.5	41.0	46.4	65.1	35.2	45.6	21.5
26.4 [1]	12.8	33.7	41.3	47.0	64.8	31.8	42.4	23.1
26.8	12.6	35.4	44.0	45.5	63.4	32.1	42.9	22.0
26.9 [1]	13.3	35.3	40.5	46.5	66.2	30.9	42.4	21.9
28.5	11.8	34.0	41.0	46.3	66.3	32.3	44.9	22.5
29.1	14.4	36.1	41.2	46.0	62.5	33.7	42.6	22.0
29.9	14.7	35.5	43.5	45.5	62.9	33.8	40.1	22.7
30.8 [1]	12.3	34.7	39.6	43.8	65.9	32.5	40.6	21.8
33.3	11.4	32.7	45.0	45.3	64.3	30.3	42.0	20.7
33.9	12.7	35.4	42.2	44.8	63.7	31.3	40.7	-------
34.0	13.2	33.2	40.3	45.3	64.1	30.6	41.2	24.1
34.0 [1]	13.2	34.1	42.9	45.3	62.9	31.8	42.9	22.6
34.4	11.6	34.9	41.0	43.6	68.6	35.8	40.7	22.1
34.6	12.4	36.7	42.2	44.8	65.9	36.1	43.9	22.8
34.7 [1]	13.4	34.0	41.8	45.8	68.3	33.4	46.7	21.0
35.1	12.2	35.6	41.0	42.7	66.7	36.8	45.6	-------
36.1	11.6	34.3	45.1	45.1	63.2	32.4	42.4	20.5
36.2 [1]	12.5	32.6	40.9	46.4	65.2	29.8	42.5	22.4
36.4	12.6	33.8	40.9	44.8	61.3	30.2	42.0	22.5
36.6	12.6	35.2	41.8	46.2	65.0	32.8	42.6	22.7
36.9	10.8	35.2	42.0	41.5	66.7	34.7	45.0	-------
37.1	10.8	35.0	41.8	43.4	66.3	34.5	45.6	-------
37.3	11.3	34.9	42.6	42.1	67.6	35.9	47.7	22.3
37.4	13.1	35.3	43.8	45.7	64.4	32.1	40.9	23.3
37.5	12.0	34.7	42.1	44.8	62.4	32.3	42.4	21.9
37.6	12.5	35.4	41.5	41.8	67.3	33.8	47.3	23.4
37.9	12.1	33.0	40.4	43.5	62.3	31.1	41.2	22.4
38.2	11.3	35.1	40.8	43.2	68.1	35.6	47.1	-------
38.5	11.9	34.8	42.6	42.6	66.2	35.1	44.4	21.3
39.0	11.8	32.3	41.3	41.8	67.9	33.8	44.9	-------
39.2	11.7	34.7	42.6	41.8	67.3	34.7	48.2	23.2
39.3	12.0	33.8	42.7	41.7	64.9	34.4	43.3	-------
39.4	13.2	34.8	42.6	45.2	63.7	31.2	41.9	-------
39.6	12.4	32.6	41.4	43.9	61.9	30.6	40.9	22.0
39.6	12.6	36.4	45.5	45.5	63.1	31.8	41.7	23.2
40.0	11.0	34.5	42.2	41.2	68.0	33.7	47.2	23.2
40.3	11.9	34.7	42.7	43.9	61.8	32.3	41.7	21.8
40.4	11.4	34.4	42.8	41.1	68.1	32.2	45.8	21.3
40.6	11.8	34.5	42.6	41.9	64.3	34.7	42.6	-------
40.9	12.2	33.5	42.3	44.0	63.8	31.1	40.8	-------
41.1	11.7	33.8	41.8	42.3	67.6	34.1	47.2	21.2
41.2	12.4	34.5	43.0	44.2	62.9	31.1	41.7	22.3
41.6	11.8	33.7	42.3	43.3	63.7	31.7	39.4	-------
41.8	12.2	34.4	41.4	43.1	67.0	34.4	46.6	20.8
42.0	12.1	34.5	44.0	44.0	63.8	31.0	42.1	21.9
42.3	12.1	35.0	44.7	44.9	63.4	32.2	42.1	21.7
42.7	11.7	34.2	43.8	41.7	66.0	34.7	46.1	21.8
42.9	11.4	35.0	43.1	42.0	67.6	35.0	46.2	-------
43.3	11.3	33.5	43.2	44.3	67.0	33.7	46.0	21.7
44.0	11.4	33.6	45.2	43.6	65.0	31.4	41.8	22.7
44.0	11.8	35.2	42.7	42.7	67.0	36.4	46.6	-------
44.9	11.6	33.2	43.7	43.7	62.8	30.7	42.1	22.5
45.0	12.2	34.7	43.3	45.1	62.2	31.1	41.8	22.0
45.1	12.2	34.6	43.2	45.7	62.3	31.5	41.0	22.4
45.3	11.0	33.6	42.2	41.7	66.2	32.7	47.0	21.9
45.5	10.8	33.4	40.9	42.6	65.5	34.3	44.6	21.5
45.6	10.7	31.8	42.5	42.8	64.5	34.4	46.7	21.3
45.7	12.0	32.8	44.0	44.2	63.0	30.4	41.1	21.7
46.5 [2]	12.7	33.5	44.3	44.7	63.7	31.0	43.2	23.7
47.1	11.7	34.2	42.7	43.9	62.8	31.2	42.0	-------
47.3	10.8	33.2	42.5	41.2	62.4	33.8	41.2	22.6
47.5	11.2	35.4	44.4	44.8	63.4	31.8	43.2	22.7
47.8	12.6	34.7	42.7	44.3	62.8	31.0	40.6	22.4
47.8	11.5	33.1	43.3	43.1	64.4	32.0	40.4	21.1
47.9	11.3	33.4	43.0	43.8	62.8	29.6	39.5	22.3
48.7	11.1	33.7	43.3	42.7	64.3	31.8	41.3	21.4
52.0	11.9	34.4	44.8	44.6	65.4	31.5	43.1	23.3
52.0	11.5	34.2	41.9	42.1	61.2	30.2	41.2	22.5
55.0	12.0	34.5	44.2	45.5	62.7	31.6	42.2	22.9
55.0	10.9	33.5	42.7	42.7	62.0	31.8	41.5	22.2
71.5	9.6	31.3	42.2	43.1	61.5	28.5	38.2	19.7
77.5	10.3	31.4	46.1	43.6	62.6	28.4	38.7	20.0

See footnotes at end of table.

TABLE 13.—*Measurements of selected body parts of 115 specimens of* Kyphosus sectatrix *and 99 specimens of* Kyphosus incisor, *expressed as percentage of standard length*—Continued

KYPHOSUS SECTATRIX—Continued

Standard length (mm.)	Percent of standard length							
	Eye diameter	Head length	Depth at pelvic fin	Snout to dorsal fin	Snout to anal fin	Snout to pectoral fin	Snout to pelvic fin	Pectoral fin length
99.5	12.0	33.9	47.7	46.5	66.3	31.2	41.2	21.9
100.5 [2]	9.0	28.0	41.0	41.0	62.2	26.7	36.9	19.4
104.5 [1]	8.9	28.3	40.5	40.2	60.3	27.3	37.6	20.9
115.0	10.2	30.0	45.7	45.2	60.9	26.6	35.8	19.2
125.0	11.1	32.0	46.6	46.2	66.7	29.8	41.1	19.8
133.0	8.3	28.6	42.5	42.1	64.4	27.7	39.5	19.5
154.5 [2]	9.9	27.8	40.5	41.7	66.3	27.2	39.2	19.4
157.5	10.2	30.0	44.4	44.8	65.1	27.0	37.9	18.4
168.5 [2]	9.7	27.7	41.8	43.1	63.8	26.9	35.9	19.6
171.0 [2]	9.7	27.5	43.3	42.0	63.7	26.5	37.7	18.9
172.5 [1]	8.7	28.2	42.6	42.0	68.1	28.7	41.2	19.5
181.5 [1]	9.3	28.7	43.5	42.7	65.6	27.5	38.6	19.7
186.5	9.5	29.5	45.6	45.4	62.2	26.5	37.3	19.6
194.0 [2]	8.6	25.5	39.7	40.0	60.6	25.8	36.1	18.5
211.0 [2]	7.5	26.8	43.1	40.3	64.0	27.5	39.3	17.9
211.0	9.6	29.4	42.9	43.8	65.9	28.7	39.1	19.1
212.0 [2]	8.7	28.3	42.7	42.5	64.6	27.4	38.2	17.3
215.5 [1]	8.4	27.1	41.0	41.3	64.3	27.3	39.1	18.2
219.0 [2]	9.2	27.9	41.9	42.7	63.2	25.8	36.3	18.4
230.0 [2]	8.8	27.6	39.6	42.6	64.1	27.8	36.7	19.3
236.5 [2]	8.2	26.8	44.4	42.9	65.1	27.3	38.1	19.0
244.0 [2]	8.3	29.1	46.7	44.9	64.5	26.0	37.1	18.6
259.0 [2]	8.2	27.6	39.6	41.7	61.8	26.8	37.1	18.3
260.0	8.2	29.0	43.5	43.8	67.7	27.5	38.8	19.6

KYPHOSUS INCISOR

Standard length (mm.)	Eye diameter	Head length	Depth at pelvic fin	Snout to dorsal fin	Snout to anal fin	Snout to pectoral fin	Snout to pelvic fin	Pectoral fin length
8.5	16.5	38.8	32.9	50.6	67.1	37.6	45.9	20.0
8.7	14.4	35.1	31.8	46.6	60.9	32.5	40.3	20.3
9.1	13.7	35.2	33.5	46.4	64.8	33.5	43.3	-------
9.8	13.3	34.6	32.4	46.1	62.2	34.7	40.7	-------
10.0	14.5	36.5	34.5	47.6	62.0	33.9	40.5	20.1
10.2	13.1	35.4	34.4	48.4	61.8	34.4	42.0	19.7
10.3	14.6	36.9	35.9	46.6	64.1	40.0	42.7	22.3
11.4	13.2	33.3	35.1	46.5	63.2	33.3	40.4	19.3
11.9	12.6	35.3	36.1	45.4	62.2	34.5	42.0	21.0
12.1	13.7	35.2	37.4	47.9	62.0	34.9	42.1	20.5
12.5	14.2	35.9	38.1	48.0	60.8	35.2	40.8	22.2
12.7 [1]	13.9	34.9	37.0	47.2	61.4	34.2	42.5	20.6
12.8	13.8	35.8	36.7	47.7	61.7	33.0	40.6	18.9
13.1	13.7	34.4	35.1	45.0	61.1	32.1	42.0	19.1
13.2	13.6	34.8	38.6	44.7	64.4	32.6	42.4	22.0
13.5	13.4	33.3	36.1	47.4	63.7	31.3	42.2	19.6
13.6	13.0	34.6	37.5	47.1	61.8	32.4	41.9	21.0
13.7	13.4	34.7	38.7	47.4	62.0	32.6	40.9	22.5
14.2	13.5	35.1	37.3	46.5	62.7	31.8	43.0	21.7
14.3	13.6	36.4	38.5	46.8	67.8	35.0	43.4	20.2
14.3	14.3	36.4	36.4	47.6	63.6	34.1	42.7	22.4
14.3	12.5	35.7	33.7	44.8	62.2	35.0	42.0	19.4
14.5	14.1	36.6	39.3	46.9	62.8	35.2	42.1	21.9
14.5	13.8	35.2	40.0	49.0	62.1	33.8	41.4	-------
14.7	13.6	36.1	38.8	45.6	62.6	34.0	42.2	22.4
14.7 [1]	13.7	35.4	36.7	47.6	67.3	33.2	41.5	20.6
15.5	13.9	36.1	37.4	46.5	62.6	32.9	43.5	22.3
15.8	12.6	33.5	34.8	45.6	63.9	32.9	41.8	-------
16.1	14.3	37.3	38.5	44.7	65.8	36.0	46.0	23.0
16.2	13.7	36.4	40.1	44.4	63.0	33.3	43.2	22.4
16.4	14.1	36.0	37.8	46.3	63.4	31.7	43.3	21.8
16.7	13.5	34.7	37.7	45.5	65.9	31.7	43.1	22.5
17.2	14.1	36.0	37.2	45.3	65.1	34.3	46.5	20.4
17.3	15.0	37.6	41.6	47.4	64.2	34.1	44.5	23.1
17.5	13.3	34.3	37.7	44.0	65.1	32.6	43.4	20.7
17.6	13.9	36.4	35.8	44.9	63.6	34.1	45.5	19.6
18.2	14.2	35.7	40.7	46.2	63.7	33.4	42.3	21.9
18.6	13.7	35.5	39.8	44.6	68.3	33.3	48.4	20.2
19.0	12.9	35.8	36.8	44.7	66.3	34.2	44.2	20.7
19.2 [1]	15.2	36.9	34.9	46.3	63.5	34.9	44.2	23.2
19.9	15.6	38.7	42.2	46.7	66.3	34.7	46.2	21.1
21.2	13.7	34.9	38.7	47.2	63.7	33.0	43.4	20.8
21.7	12.4	34.1	39.6	46.5	65.0	31.3	42.4	19.4
22.0	12.0	32.7	37.3	43.6	66.8	33.6	46.4	21.1
23.3	12.8	34.8	42.5	45.1	64.4	33.0	43.3	20.9
23.4	12.4	33.8	39.7	46.6	62.8	30.8	41.5	23.1
23.5	14.0	34.0	37.0	46.8	64.7	32.3	41.3	22.1
23.9	13.8	33.9	39.7	46.9	61.5	30.5	41.0	21.8
24.2	11.9	33.9	38.8	43.4	65.7	32.2	46.7	19.9
24.4	14.8	37.3	37.7	45.9	-------	35.7	43.0	22.1
24.7	13.3	34.0	42.5	-------	66.0	32.8	43.3	21.0

TABLE 13.—*Measurements of selected body parts of 115 specimens of* Kyphosus sectatrix *and 99 specimens of* Kyphosus incisor, *expressed as percentage of standard length*—Continued

KYPHOSUS INCISOR—Continued

Standard length (mm.)	Percent of standard length							
	Eye diameter	Head length	Depth at pelvic fin	Snout to dorsal fin	Snout to anal fin	Snout to pectoral fin	Snout to pelvic fin	Pectoral fin length
24.8	14.1	36.7	39.1	44.0	68.1	33.9	48.0	23.4
25.4	12.6	35.4	40.2	44.1	63.8	33.9	44.9	20.9
25.4	11.4	33.9	35.4	44.9	61.0	33.9	43.3	20.5
25.5	12.9	32.9	40.4	47.5	63.5	32.5	43.1	23.5
25.8	13.2	35.7	39.5	45.0	64.0	33.7	44.6	22.1
26.3	13.3	33.1	40.7	44.5	66.2	33.5	45.2	22.0
27.4	11.5	32.8	38.3	44.5	65.7	31.7	43.1	19.7
27.5	12.7	33.5	41.8	45.1	63.6	30.2	40.4	22.5
27.7	13.0	35.0	42.2	43.7	65.7	34.7	45.1	22.4
28.0	12.9	36.4	43.6	43.9	61.4	31.8	41.4	21.1
28.4	11.2	31.7	43.3	44.0	64.8	30.6	42.6	21.8
28.6	14.0	36.0	40.6	47.2	64.0	32.5	43.4	21.7
28.6	11.9	31.8	40.9	44.1	63.3	28.7	40.9	22.7
29.6	11.8	33.4	38.9	42.9	64.9	34.1	42.9	22.0
29.7	12.4	33.7	40.1	46.5	62.0	31.0	42.4	19.9
29.8	12.4	34.2	38.9	43.0	63.4	33.6	42.3	23.8
30.8	11.7	31.8	40.9	44.5	61.4	30.2	39.6	23.1
31.0	11.9	31.3	41.6	42.3	62.9	30.0	39.7	21.6
32.5	12.9	32.6	39.4	45.5	61.5	30.8	41.5	22.1
33.6	11.9	32.4	43.7	46.4	64.0	29.8	42.0	20.8
34.5	12.6	33.9	43.5	47.5	62.6	31.0	42.6	22.3
35.1	12.8	34.8	42.2	45.6	61.8	32.8	41.9	21.7
35.2	13.1	34.1	41.5	44.9	61.6	31.5	41.5	23.0
37.0	11.9	33.8	41.6	45.1	63.5	31.6	42.4	21.9
37.5	11.6	31.7	40.3	44.5	63.2	30.4	42.1	21.3
37.5	12.3	31.5	42.1	45.9	59.7	29.9	40.5	22.1
38.0	11.8	33.2	38.4	43.9	61.1	30.5	39.5	21.3
38.2	11.0	32.5	40.8	------	64.7	33.0	46.9	22.3
38.3	11.5	32.1	41.5	44.6	61.9	29.2	41.0	21.1
38.7	12.7	34.4	39.5	42.1	61.5	34.6	42.6	------
38.8	12.4	34.8	41.0	45.1	62.6	32.2	44.3	21.1
39.1	12.3	35.0	44.8	43.7	63.4	32.2	42.2	21.5
41.5	11.3	35.7	44.1	44.1	64.3	30.4	42.4	22.2
44.2	12.4	33.9	41.6	45.5	62.2	30.8	40.5	22.4
44.5	11.5	33.3	43.6	43.1	62.2	30.3	41.8	22.2
44.5	11.7	33.0	38.9	40.9	64.5	32.8	46.3	22.5
45.2	10.8	33.6	43.4	43.4	63.7	30.3	42.7	21.9
45.2	11.9	32.1	41.4	42.0	61.3	29.0	39.4	22.1
45.5	11.2	36.0	44.4	44.2	63.7	30.5	41.5	21.5
50.0	10.4	32.4	41.6	44.6	63.8	32.4	45.2	20.4
54.5 [1]	11.7	33.3	41.5	45.0	62.8	30.6	42.2	22.6
58.5	10.9	32.1	42.1	41.9	63.2	29.4	39.3	21.7
101.5	8.9	28.9	41.9	42.8	58.0	27.1	38.4	20.9
184.5	7.7	26.0	39.8	38.8	60.7	25.5	36.3	17.5
192.0	8.2	26.3	40.4	41.7	62.5	26.0	37.0	17.7
233.0 [2]	8.4	28.1	40.8	42.9	61.4	25.5	35.2	18.2
239.0	6.9	25.7	41.0	39.1	63.0	24.5	35.8	16.9
252.0 [2]	7.9	27.4	40.3	39.9	64.1	27.4	39.9	17.3

[1] Specimens from northern Bahamas (including Antilles Current and excluding Florida Current.

[2] Specimens captured beyond the Atlantic coast of the United States and the northern Bahamas.

KEY TO THE NORTH ATLANTIC SPECIES OF *KYPHOSUS*

This key is designed for specimens larger than about 16 mm., approximately the size at which gill rakers are sufficiently formed to be used in separation (fig. 21). The dorsal and anal soft-rays may be used in separation of specimens as small as 8.5 mm. (fig. 20).

A. Total dorsal and anal soft-rays, 23 or 24 (rarely 21 or 22). Dorsal rays, 12 (rarely 11 or 13). Anal rays, 11 (rarely 9 or 12). Gill rakers on first arch; lower limb, 17 or 18 (rarely 16 or 19); entire arch, 22 to 26 (rarely 27); ceratobranchial bone, 12 or 13 (rarely 11) under 150 mm. and 13 or 14 over 150 mm.
Kyphosus sectatrix (Linnaeus).

B. Total dorsal and anal soft-rays, 25 to 27 (rarely 28). Dorsal rays, 13 or 14 (rarely 15). Anal rays 12 or 13. Gill rakers on first arch; lower limb, 19 to 22 (rarely 23); entire arch, 25 to 30 (rarely 31); ceratobranchial bone, 14 or 15 (rarely 13) under 150 mm. and 15 over 150 mm.
Kyphosus incisor (Cuvier).

DISTRIBUTION ALONG THE ATLANTIC COAST OF UNITED STATES AND NORTHERN BAHAMAS

The extension of records of *K. incisor* north to Cape Cod makes the northern known range in the western North Atlantic the same for both *K. sectatrix* and *K. incisor*. Juveniles of both species were frequently caught under the same patch of *Sargassum;* however, Longley and Hildebrand (1941) reported the adults of *K. sectatrix* and *K. incisor* to school around different coral reefs at Tortugas, Fla.

There is little apparent difference in the length of spawning season. In the Bahamas, 8 *K. sectatrix* less than 40 mm. were taken in the winter; the only specimens of *K. incisor* less than 40 mm. were taken in the summer (figs. 5 and 11).

LITERATURE CITED

ANDERSON, WILLIAM W.
1957. Early development, spawning, growth, and occurrence of the silver mullet (*Mugil eurema*) along the south Atlantic coast of the United States. U.S. Department of the Interior, Fish and Wildlife Service, Fishery Bulletin, No. 119, vol. 57, p. 397–414.

ANDERSON, WILLIAM W., and JACK W. GEHRINGER.
1957a. Physical oceanographic, biological, and chemical data south Atlantic coast of the United States *Theodore N. Gill* cruise 3. U.S. Department of the Interior, Fish and Wildlife Service, Special Scientific Report—Fisheries No. 210. 208 p.

1957b. Physical oceanographic, biological, and chemical data south Atlantic coast of the United States M/V *Theodore N. Gill* cruise 4. U.S. Department of the Interior, Fish and Wildlife Service, Special Scientific Report—Fisheries No. 234. 192 p.

1958a. Physical oceanographic, biological, and chemical data south Atlantic coast of the United States M/V *Theodore N. Gill* cruise 5. U.S. Department of the Interior, Fish and Wildlife Service, Special Scientific Report—Fisheries No. 248. 220 p.

1958b. Physical oceanographic, biological, and chemical data south Atlantic coast of the United States

M/V *Theodore N. Gill* cruise 6. U.S. Department of the Interior, Fish and Wildlife Service, Special Scientific Report—Fisheries No. 265. 99 p.

1959a. Physical oceanographic, biological, and chemical data south Atlantic coast of the United States M/V *Theodore N. Gill* cruise 7. U.S. Department of the Interior, Fish and Wildlife Service, Special Scientific Report—Fisheries No. 278. 277 p.

1959b. Physical oceanographic, biological, and chemical data south Atlantic coast of the United States M/V *Theodore N. Gill* cruise 8. U.S. Department of the Interior, Fish and Wildlife Service, Special Scientific Report—Fisheries No. 303. 227 p.

1959c. Physical oceanographic, biological, and chemical data south Atlantic coast of the United States M/V *Theodore N. Gill* cruise 9. U.S. Department of the Interior, Fish and Wildlife Service, Special Scientific Report—Fisheries No. 313. 226 p.

Anderson, William W., Jack W. Gehringer, and Edward Cohen.

1956a. Physical oceanographic, biological, and chemical data south Atlantic coast of the United States M/V *Theodore N. Gill* cruise 1. U.S. Department of the Interior, Fish and Wildlife Service, Special Scientific Report—Fisheries No. 178. 160 p.

1956b. Physical oceanographic, biological, and chemical data south Atlantic coast of the United States *Theodore N. Gill* cruise 2. U.S. Department of the Interior, Fish and Wildlife Service, Special Scientific Report—Fisheries No. 198. 270 p.

Baird, S[pencer] F.

1873. List of fishes collected at Woods Hole. U.S. Commission of Fish and Fisheries. Part 1. Report on the condition of the sea fisheries of the south coast of New England in 1871 and 1872. p. 823–827.

Bean, Barton A.

1905. Fishes of the Bahama Islands. In The Bahama Islands. Geographical Society of Baltimore, Johns Hopkins Press, p. 293–325.

Bean, Tarleton H.

1897. Notes upon New York fishes received at the New York aquarium, 1895–1897. American Museum of Natural History, Bulletin 9, article 24, p. 327–375.

1903. Catalogue of the fishes of New York. New York State Museum, No. 60, Zoology 9. 784 p.

Bowdich, [Sarah].

1825. III Appendix: Containing zoological and botanical descriptions, and translations from the arabic. Fishes of the Gambia, p. 233–238. In Bowdich, T[homas] Edward. 1825. Excursions in Madeira and Porto Santo during the Autumn of 1823, while on his third voyage to Africa. George B. Whittaker, London.

Carvalho, J. Paiva.

1950. Resultados cientificos do cruzeiro do "Baependi" e do "Vega" a I. da Trindade (Peixes). Boletim do Instituto Paulista de Oceanografia, Sao Paulo, Brasil. Vol. 1, no. 1, p. 97–133. [In Brazilian Portuguese with English summary.]

Catesby, Mark.

1743. The natural history of Carolina, Florida, and the Bahama Islands: containing the figures of birds, beasts, fishes, serpents, insects and plants, etc. Vol. 2, 1st edition, London. 31 p.

Cuvier, [Georges], and [Achille] Valenciennes.

1831. Histoire naturelle des poissons. Vol. 7, F. G. Levrault, Paris. 531 p.

Doderlein, P[ietro].

1884. Rinvenimento di una specie di pesce dell' esotico genere *Pimelepterus* Lac. nelle acque del golfo di Palermo. Il Naturalista Siciliano, Giornale di Scienze Naturali. Third Year, (1883–84), Virzi, Palermo, p. 81–86.

Evans, Howard E.

1948. Cleaning and staining small invertebrates, in toto, for demonstrating ossification. Turtox News. Vol. 26, no. 2, p. 42–47.

Evermann, Barton Warren, and William Converse Kendall.

1900. Check-list of the fishes of Florida. U.S. Commission of Fish and Fisheries. Part 25. Report of the Commissioner for the year, ending June 30, 1899, p. 37–103.

Evermann, Barton Warren, and Millard Caleb Marsh.

1900. The fishes of Porto Rico. U.S. Fish Commission, Bulletin, vol. 20, Part 1, p. 49–350.

Fowler, Henry W.

1915. Cold-blooded vertebrates from Florida, the West Indies, Costa Rica, and eastern Brazil. Academy of Natural Sciences of Philadelphia, Proceedings, p. 244–269.

1917. Notes on New England fishes. Boston Society of Natural History, Proceedings, 1914–20, vol. 35, no. 4, p. 109–138.

1929. Notes on percoid and related fishes. Academy of Natural Sciences of Philadelphia, Proceedings, vol. 81, p. 633–657.

1944. The fishes. Results of the fifth George Vanderbilt expedition (1941). (Bahamas, Caribbean Sea, Panama, Galapagos Archipelago and Mexican Pacific islands). Academy of Natural Sciences of Philadelphia, Monographs, No. 6, p. 75–583.

1945. A study of the fishes of the southern peidmont and coastal plain. Academy of Natural Sciences of Philadelphia, Monographs, No. 7, 408 p.

1952. A list of the fishes of New Jersey, with off-shore species. Academy of Natural Sciences of Philadelphia, Proceedings, vol. 104, p. 89–151.

1953. The shore fishes of the Colombian Caribbean (Ictiologia). Instituto de Ciencias Naturales de la Universidad Nacional de Colombia—Bogota, Boletin, vol. 6, no. 27, Caldasia, p. 43–73.

Gmelin, Jo[hann] Frid[erick].

1789. Caroli a Linnè . . . Systema Naturae. Tomus primus, Editio decima tertia, aucta, reformata. Classis pisces, Lugbuni Apud J. B. Della-molliere, Pars III, p. 1126–1516.

Goode, G[eorge] Brown.

1879. A preliminary catalogue of the fishes of the St. Johns River and the east coast of Florida. With descriptions of a new genus and three new species. U.S. National Museum, Proceedings, vol. 2, p. 108–121.

Günther, Albert.

1859. Catalogue of the acanthopterygian fishes in the collection of the British Museum. Gasterosteidae, Berycidae, Percidae, Aphredoderidae, Pristipomatidae, Mullidae, Sparidae. Vol. 1. 524 p.

Hildebrand, Samuel F., and William C. Schroeder.

1928. Fishes of Chesapeake Bay. U.S. Bureau of Fisheries, Bulletin, vol. 43 (1927), part 1, Document 1024. 388 p.

Hollister, Gloria.

1934. Clearing and dyeing fish for bone study. New York Zoological Society, Zoologica, vol. 12, No. 10, p. 89–101.

Jordan, David S.

1884. List of fishes collected at Key West, Florida, with notes and descriptions. U.S. National Museum, Proceedings, vol. 7, p. 103–150.

Jordan, David Starr, and Barton Warren Evermann.

1898. The fishes of North and Middle America: A descriptive catalogue of the species of fishlike vertebrates found in the waters of North America, north of the Isthmus of Panama. U.S. National Museum, Bulletin No. 47. Part 2, p. 1241–2183.

1927. New genera and species of North American fishes. California Academy of Sciences, Proceedings, series 4, vol. 16, No. 15, p. 501–507.

Jordan, David Starr, Barton Warren Evermann, and Howard Walton Clark.

1930. Check list of the fishes and fishlike vertebrates of North and Middle America north of the northern boundary of Venezuela and Colombia. U.S. Commissioner of Fisheries, Report for the fiscal year 1928. Part 2, appendix 10, Bureau of Fisheries, Document 1055. 670 p. [Reprinted.]

Jordan, David Starr, and Bert Fesler.

1893. A review of the sparoid fishes of America and Europe. U.S. Commission of Fish and Fisheries, Report of the Commissioner for 1889–1891, p. 421–544.

Jordan, David S., and Charles H. Gilbert.

1879. Notes on the fishes of Beaufort Harbor, N.C. U.S. National Museum, vol. 1(1878), p. 365–388.

1881. Notes on a collection of fishes, made by Lt. Henry E. Nichols, U.S.N., on the west coast of Mexico, with descriptions of new species. U.S. National Museum, Proceedings, vol. 4, p. 225–233.

Jordan, D[avid] S., and C[harles] H. Gilbert.

1883. On certain neglected generic names of Lacépède. U.S. National Museum, Proceedings, vol. 5(1882), p. 570–576.

Jordan, David Starr, and Joseph C. Thompson.

1905. The fish fauna of the Tortugas Archipelago. U.S. Bureau of Fisheries, Bulletin, vol. 24(1904), p. 231–256.

Kendall, William C.

1908. Fauna of New England. 8. List of the pisces. Boston Society of Natural History, Occasional Papers, No. 7. 152 p.

Lacépède, [Bernhard G. E.].

1802. Histoire naturelle des poissons. Tome Troisième, Chez Plassan, Paris. 558 p.

1803. Histoire naturelle des poissons. Tome Quatrième, Chez Plassan, Paris. 728 p.

Lee, Thomas.

1889. List of fishes taken by steamer *Albatross* among Bahama Islands and at Nassau fish-market during March and April 1886. U.S. Fish Commission Report, part 14(1886), p. 669–672.

Linnaeus, Carl.

1758. Systema naturae. Editio decima, Reformata Tomus I, Laurentii Salvii, Holmiae. 824 p.

1766. Systema naturae. Editio duodecima, Reformata Tomus I, part 1, Laurentii Salvii, Stockholm. 532 p.

Longley, William H., and Samuel F. Hildebrand.

1941. Systematic catalogue of the fishes of Tortugas, Florida, with observations on color, habits, and local distribution. Carnegie Institution of Washington, publication 535, Tortugas Laboratory, Papers, vol. 34. 331 p.

Mansueti, Romeo [J.].

1958. The development of anal spines and soft-rays in young striped bass, *Roccus saxatilis*. Maryland Department of Research and Education, Contribution No. 113. 12 p.

Meek, Seth E., and Samuel F. Hildebrand.

1925. The marine fishes of Panama. Field Museum of Natural History, Chicago, Publication 226, Zoological Series, vol. 15, part 2, p. 330–707.

Metzelaar, J.

1919. Report on the fishes, collected by Dr. J. Boeke in the Dutch West Indies, 1904–1905, with comparative notes on marine fishes of tropical west Africa. Rapport Betreffende een voorloopig onderzoek naar den toestand van de Visscherij en de Industrie van Zeeproducten in de Kolonie Curacao. 316 p.

Miranda Ribeiro, A[lipio] de.

1919. A fauna vertebrada da Ilha da Trindade. Archivos do Museu Nacional do Rio de Janeiro, vol. 22, p. 171–179. [In Brazilian Portuguese.]

Mowbray, Louis S.

1949. The commercial and game fishing industries of Bermuda. A paper prepared . . . for the Gulf and Caribbean Fisheries Institute held at Miami Beach, Florida, November, 1949. 19 p.

Nichols, J[ohn] T., and C[harles] M. Breder, Jr.

1927. The marine fishes of New York and southern New England. New York Zoological Society, Zoologica, vol. 9, No. 1. 192 p.

Parr, Albert Eide.

1930. Teleostean shore and shallow-water fishes from the Bahamas and Turks Island. Bingham Oceanographic Collection, Bulletin, Peabody Museum of Natural History, Yale University, vol. 3, article 4. 148 p.

POEY, FELIPE.
1866. Repertorio fisico—natural de la Isla de Cuba. Revista de los tipos Cuvierianos y Valenciennianos correspondientes a los peces de la Isla de Cuba. Havana, Tomo 1, p. 308–338.

ROSEN, NILS.
1911. Contributions to the fauna of the Bahamas. III. The Fishes. Lunds Universitets Arsskrift, Ny Foljd, afd. 2, bd. 7, nr. 5, p. 46–72.

SMITH, HUGH M.
1898. Fishes found in the vicinity of Woods Hole. U.S. Fish Commission, Bulletin, vol. 17 (1897), p. 85–111.

1907. The fishes of North Carolina. North Carolina Geological and Economic Survey, vol. 2. 453 p.

TORTONESE, ENRICO.
1954. Pesci rari e interessanti dei mari di Sicilia. Conserve e Derivati Agrumari, Palermo, vol. 3, No. 10, April–June, 1954, p. 79–83.

TOWNSEND, CHARLES HASKINS.
1929. Records of changes in color among fishes. New York Zoological Society, Zoologica, vol. 9, No, 9, p. 321–378.

TRUITT, REGINALD V., BARTON APPLER BEAN, and HENRY W. FOWLER.
1929. The fishes of Maryland. Maryland Conservation Bulletin, No. 3. 120 p.

U. S. DEPARTMENT of COMMERCE, COAST and GEODETIC SURVEY.
1955. Surface water temperatures at tide stations Atlantic Coast North and South America. Special Publication No. 278, 5th edition (with data through 1954), U.S. Department of Commerce, Coast and Geodetic Survey, Washington. 69 p.

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RAFT CULTURE OF OYSTERS IN MASSACHUSETTS

By WILLIAM N. SHAW

March 3. 1849

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ABSTRACT

The harvest of oysters in Massachusetts has dropped more than 50 percent in the last 50 years. The possibility of growing oysters attached to rafts was tested as a method of culture that might be useful in reviving the declining oyster industry.

Oysters suspended from rafts grew about twice as fast as oysters growing on the bottom. Survival of raft oysters was about 6 times greater than that of bottom-grown oysters. This study showed that oysters can reach market size in 2½ years, if they are first suspended from a raft for 14 months. During the final year, raft-grown oysters should be placed on the bottom to let the shells thicken. Normally, wild oysters take from 4 to 5 years to reach market size in Cape Cod waters.

A gross profit of $3.75 per bushel was earned from the raft-grown oysters. This amount compares favorably with the present gross profit of $4.50 per bushel earned by local oystermen who grow oysters on the bottom.

This experiment demonstrates that raft culture is commercially feasible in Massachusetts.

RAFT CULTURE OF OYSTERS IN MASSACHUSETTS

By William N. Shaw, *Fishery Research Biologist*

BUREAU OF COMMERCIAL FISHERIES

The harvest of oysters in the United States has dropped more than 50 percent during the past 50 years. For the decade 1893–1902, the annual harvest of oyster meats averaged 164.9 million pounds, but for 1943–52 it was only 76.8 million pounds (Galtsoff, 1956). An even greater decrease has occurred in Massachusetts. Figure 1 shows that in this State the annual average harvest of 1,222,500 pounds of oyster meats during the ten year period 1910–19 has fallen to the present low level of 204,700 pounds (1950–59), a decline of 83.3 percent. Since 1952 this trend has continued at a substantially higher rate and only 113,000 pounds were harvested in 1958, an all-time low for the State (fig. 2).

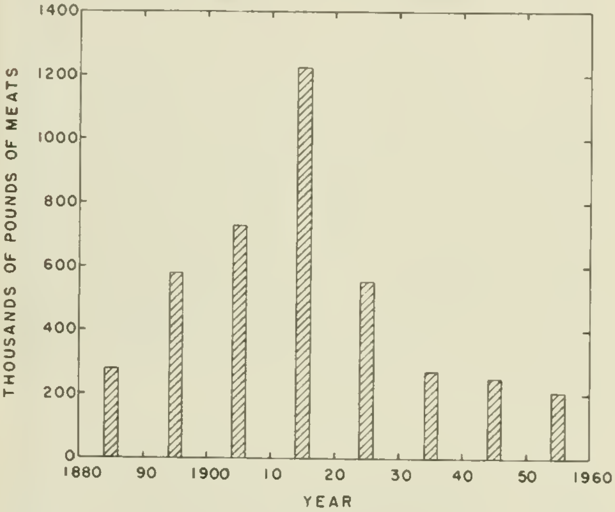

FIGURE 1.—Ten-year annual average of oysters marketed in Massachusetts, 1880–1960.

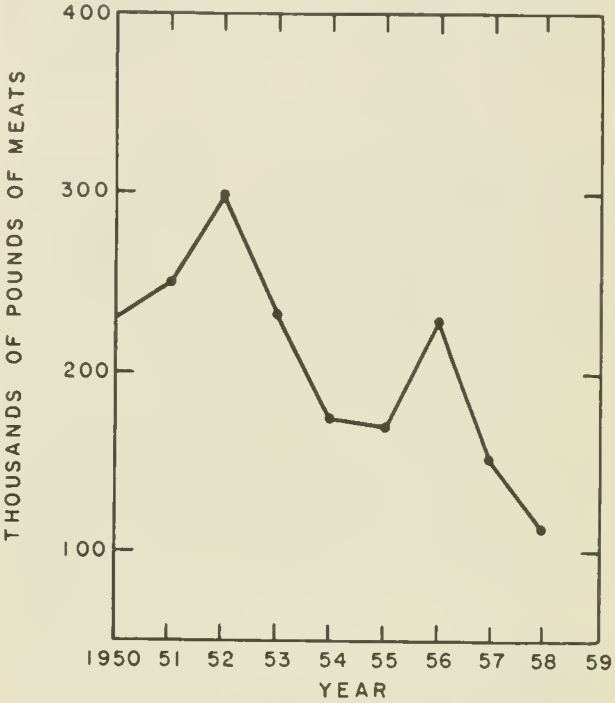

FIGURE 2.—Annual harvest of oysters in Massachusetts, 1950–58.

I wish to thank Dr. Paul S. Galtsoff for assistance in organizing the project and for suggestions in preparing the manuscript; J. C. Hammond, commercial oyster grower, whose help in construction and maintenance of the raft made this project possible; Gilbert Covell, commercial oyster grower, who donated young oysters for the observations. The late Charles Jones, former Chatham shellfish warden, gave permission to use certain areas where oyster spat could be caught. Without the cooperation of local oyster growers and officials the project could not have been carried out. Robert K. Brigham furnished the photographs and Frank A. Bailey made the drawings.

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HISTORY OF MASSACHUSETTS OYSTER INDUSTRY

The Massachusetts oyster industry is centered around Cape Cod. When the first settlers came to this area they found many natural oyster beds in the tidal rivers emptying into Buzzards Bay, Cape Cod Bay, and Nantucket Sound. Since most of the beds were easily accessible at low tides it was not long before the Cape's natural supply of oysters was greatly reduced. Many towns recognized the value of oyster-beds and for fear of their destruction passed laws intended to protect the oyster fishery. As early as 1772 the town of Wellfleet regulated the taking of oysters in Billingsgate Bay. By 1775 Wareham invoked a law, "that there should be no shellfish nor shell sold or carried out of the town." Other restrictions pertaining to the taking of shellfish were inaugurated, but in most cases the laws were passed too late or provided only temporary relief; the destruction of many natural beds had already taken place.

The next phase in the history of the industry began during the early 1840's with the planting of Virginia oysters on leased grounds at Wellfleet. By 1850, 100,000 bushels were planted (Ingersoll, 1881). Because of the Civil War (1861–65) there was a sharp decline in the shipping of oysters. After the war, the decline continued until in 1880 only 6,000 bushels of Virginia oysters were planted in Wellfleet.

With the decline of the importation of Virginia stock, a system of grants was developed. In 1874 the towns of Swansea and Somerset were given the privilege of issuing grants for the propagation of oysters. Four years later, in 1878, the Massachusetts oyster laws were amended giving the mayor, aldermen, or selectmen of each city and town the right to issue grants "for a term not exceeding 20 years to an inhabitant thereof, to plant, grow, and dig oysters."

The oyster industry of Massachusetts has not changed significantly since the first grants were issued. Under this system the oysterman leases from a town a certain area of suitable offshore bottom. In the spring he plants fully grown oysters obtained from the waters of other States, mainly from Connecticut. The majority of these oysters are sold in the late fall and winter; only those under the 3-inch minimum legal size are left on the bottom for another year.

Because of the recent scarcity of oysters in Long Island Sound, the Connecticut and New York growers can no longer supply Massachusetts with enough bedding stock; therefore, many Bay State oystermen have gone out of business. For example, in Oyster Pond River, Chatham, where 20 men were once in the oyster business, only 3 are working at present. Since the oyster industry of Massachusetts can no longer afford to rely on obtaining bedding stock from other States, new and more effective methods of oyster culture are needed, if the industry is to prosper.

UTILIZATION OF THE POTENTIAL SEED RESOURCES

At present the potential seed resources of the Cape are not utilized. Wild oysters are found in the tidal waters of Cape Cod indicating that natural reproduction is taking place. Waters around Wareham River and Onset Bay are capable of producing thousands of bushels of seed oysters if proper spat-collecting methods are used. Failures of setting in this area are rare (Galtsoff, Prytherch, and McMillin, 1930). Good setting regions are also found along the south shore of Cape Code where many wild oyster sets occur nearly every year. By taking advantage of these resources, the local oyster industry could be made self-sustaining instead of depending on the importation of out-of-State bedding stock; by raising seed a true oyster culture would be practiced.

The basic reason for the present lack of utilization of Massachusetts natural seed is its slow growth. Local production is hampered by high mortality from predation, and difficulty in obtaining grants for the culturing of seed oysters. Massachusetts is near the northern limit of the range of distribution of the eastern oyster, *Crassostrea virginica*, which according to Abbott (1954), extends along the coast of the United States from the Gulf of St. Lawrence to the Gulf of Mexico. In Cape Cod waters wild oysters reach market-size (3-in. or greater) in 4 to 5 years, although fishermen report that in Wellfleet oysters grow to market size in 3½ years. During this time they are the prey of enemies. Our records show that of 400 bushels of seed oysters planted in Oyster Pond River in the fall of 1956, nearly 100-percent mortality had occurred by the end of 1958 due mainly to drills and whelks. Many growers throughout the State report similar experiences in attempting to raise oysters from spat.

Oystermen, who are willing to utilize the State seed resources, experience difficulty in obtaining new grants. At present, each coastal community has jurisdiction over the shellfisheries of its tidal water and restricts the issuing of grants to the residents. Furthermore, the officers of coastal municipalities are reluctant to make available any new grounds to private individuals for oyster cultivation. Finally, an oysterman has no assurance that his grant will be renewed at the expiration of the lease. Slow growth of oysters, high mortality, and the difficulty of obtaining permanent grants discourage him from investing his time and money in growing oysters by the present slow methods.

GROWING OYSTERS OFF BOTTOM

Experiments successfully tried in the United States, Canada, Australia, and Japan have shown that oysters grow faster when lifted off the bottom. In Elkhorn Slough, Monterey Co., Calif., Bonnot (1935) obtained remarkably rapid growth of Japanese seed oysters, *Crassostrea gigas*, which reached market-size in only 8 months. Some Eastern (U.S.) oysters in this experiment grew well but at a slower rate than the Japanese species. Similar studies were conducted at Ladysmith, British Columbia, Canada. One-year-old Japanese oysters were hung from rafts in March and by November were large enough to harvest. Quayle (1956) reports that by this method oysters can be harvested in two years instead of three.

In Japan and Australia, oysters are cultured off bottom on a commercial scale. In the Inland Sea of Japan, 20 million pounds of oyster meats are harvested annually using bamboo rafts (Wallace, 1959). Australian oystermen grow many of their oysters in wooden trays kept above the bottom (Kesteven, 1947). Despite the success of off-bottom culture in Japan and Australia, this method had not been adopted to any extent by commercial growers in the United States.

PURPOSE OF THE STUDY

To develop a method of oyster culture which might be useful in reviving the Massachusetts oyster industry, and at the same time utilize the State seed resources, the U.S. Bureau of Commercial Fisheries at Woods Hole began studies on the growth and survival of oysters kept on rafts in Oyster Pond and Oyster Pond River, at Chatham (Mass.). The present paper summarizes the observations made between 1956 and 1959. Particular attention was given to whether the benefits obtained from the cultivation of raft-grown oysters would justify the possible additional cost of production.

LOCALITY AND DESCRIPTION OF THE AREA

Oyster Pond (fig. 3) is approximately three-fourths of a mile long and one-quarter of a mile wide. Its bottom along the shore is hard sand which changes to soft mud in deeper water. Records show that natural oyster beds once existed in the pond, but by 1877, all had disappeared (Belding, 1909).

Oyster Pond River (fig. 3) begins at the outlet of the pond where it runs SW. for seven-eighths of a mile and then bends to a SE. direction for another three-quarters of a mile before emptying into Stage Harbor. The width of the river is fairly constant throughout its entire length, averaging about 165 yards. The depth varies from 1 to 9 feet at mean low water except for a 10-foot channel. Tidal currents recorded with a Gurley current meter are about 2 feet per second during flood tide. The bottom is generally hard-packed sand, but in deeper water away from the shore and in areas where tidal creeks flow into the river, the bottom is soft with a high percentage of silt and clay. High cliffs are found along the entire length of the north side of the river, and for the first seven-eighths of a mile on the south side, but for the remaining three-quarters of a mile only tidal flats appear.

TEMPERATURE, SALINITY, OXYGEN CONTENT, AND pH OF WATER

Surface water temperature in Oyster Pond River was recorded during each visit to the site. In addition, a thermograph was installed from April 1 to November 20, 1958. During 1958 the average monthly temperature fluctuated from 1.2° C. in February to a high of 22.3° C. in July, and then to a low of 0.8° C. in December (fig. 4). The water temperature was also found to vary during the day. For example, on April 24, 1958, a low of 11.8° C. was recorded at 6:00 a.m. By 12:00 noon the temperature had climbed to 16.2° C. In the

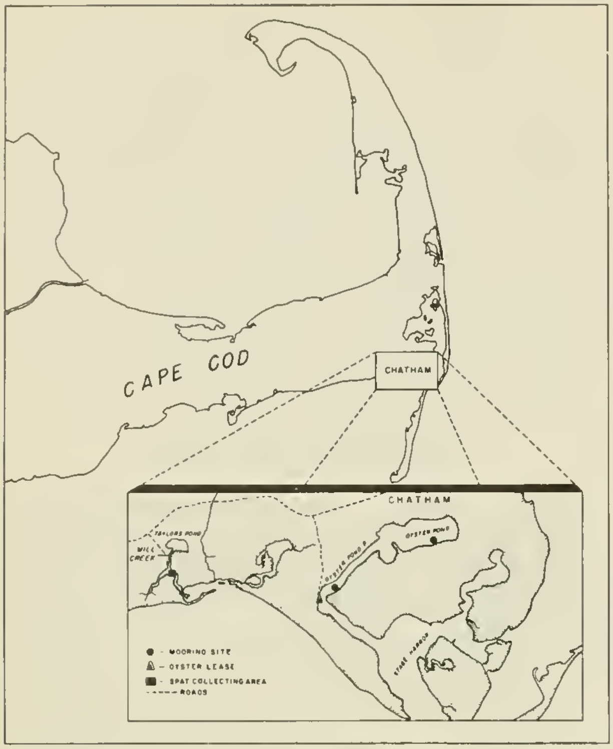

Figure 3.—Locations of mooring sites, oyster leased grounds, and spat collecting area near Chatham, Mass.

afternoon the temperature dropped slowly and by 6:00 p.m. it was down to 13.4° C.

During the 3 years of observations the salinity of the water in Oyster Pond River varied from 29.23‰ to 32.68‰. Since there is no major fresh-water drainage entering the river, a horizontal salinity gradient is absent. The salinity (fig. 4) was higher (31.00–32.68) from June 1956–October 1957 than for the period November 1957–December 1958 (29.23–31.00).

Dissolved oxygen (fig. 4) was highest during the winter and lowest in the summer. Most of the readings were at or near 100 percent saturation. The pH varied from 7.6 to 8.0.[1]

AQUATIC LIFE IN THE RIVER

The most conspicuous or most abundant animals and plants found on or near the oyster bottoms are various species of algae, Bryozoa, Arthropoda, and Mollusca. All the animals species listed in the table are permanent residents of Oyster Pond River with the exception of the horseshoe crab, *Limulus polyphemus*, which enters the river in early spring. After it spawns, *polyphemus* leaves the river for deeper water.

The most common algae and invertebrates collected or recorded from Oyster Pond River (Mass.) are:

Algae:[1]
- Enteromorpha sp.
- Gracilaria confervoides
- Griffithsia sp.
- Ceramium rubrum
- Chondria sp.
- Champia parvula
- Scythosiphon lomentaria

Porifera:
- Microciona prolifera

Bryozoa:[2]
- Membranipora tenuis
- Electra hastingsae
- Callopora aurita
- Schizoporella unicornis
- Schizoporella biaperta
- Cryptosula pallasiana
- Hippodiplosia pertusa
- Microporella ciliata
- Parasmittina trispinosa

Arthropoda:
- Libinia emarginata
- Carcinides maenas

Arthropoda—(Continued)
- Cancer irroratus
- Neopanopeus texana
- Panopeus herbstii
- Limulus polyphemus

Mollusca:
- Littorina litorea
- Nassarius obsoletus
- Urosalpinx cinerea
- Eupleura caudata
- Busycon canaliculatum
- Busycon carica
- Polinices duplicatus
- Crepidula fornicata
- Aequipecten irradians
- Mercenaria (Venus) mercenaria
- Anomia simplex
- Crassostrea virginica
- Mytilus edulis
- Modiolus demissus
- Mya arenaria
- Gemma gemma

Tunicata:
- Botryllus schlosseri
- Molgula manhattensis

[1] Algae identified by Dr. Paul S. Galtsoff from material collected on August 7, 1951.

[2] Bryozoa identified by Mrs. M. B. Lambert from a sample taken after dredging in 5 to 8 feet of water on July 14, 1953.

Several species of oyster predators are abundant. These include the oyster drills, *Urosalpinx cinerea* and *Eupleura caudata*, and two species

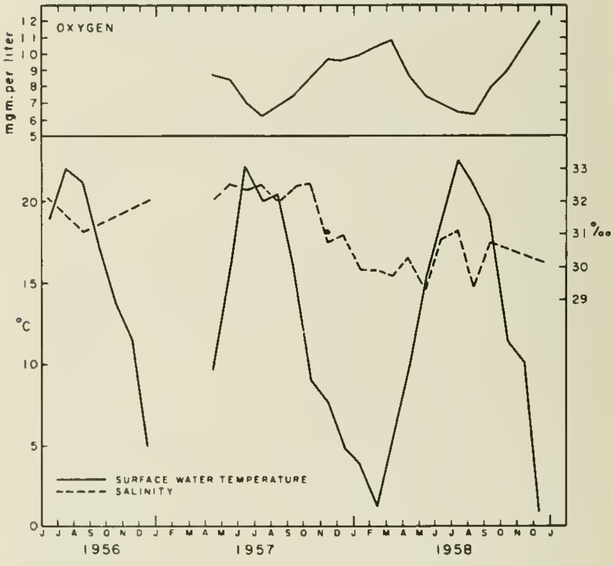

Figure 4.—The average monthly water temperature, salinty, and content of dissolved oxygen for Oyster Pond River.

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[1] Corrected for salt error.

of whelks, *Busycon carica* and *B. canaliculatum*. All four occur on the oyster grounds throughout the year and inflict a considerable amount of damage. Noticeably absent in the river is the starfish, *Asterias forbesi*. Only a few specimens were found in the lower stretches of the river during the three years of investigation.

It is of interest to mention the fluctuation in the abundance of the green crab, *Carcinides maenas*. In the spring of 1957, the crabs were found in such great numbers that they were caught by commercial fishermen for bait. By 1958 the population of crabs had so declined that commercial fishing became unprofitable and was terminated after the first day. In 1959, only an occasional green crab was observed in the river.

Two species of algae were conspicuous. *Gracilaria confervoides* was found on the oyster shells on the bottom, and *Enteromorpha* sp. was the principal fouling plant on the oysters attached to the raft. Other major fouling organisms included the compound ascidian, *Botryllus schlosseri*, the simple ascidian, *Molgula manhattensis*, and the barnacle, *Balanus balanoides*. The most abundant bryozoan was *Schizoporella unicornis*. Second in abundance were the peculiar nodular colonies of *Parasmittina trispinosa* found in soft mud in the channel and oyster bottom.

Throughout the tidal flats wild oysters grow attached to the stems of marsh grass, and often are found on exposed rocks; some set on ribbed mussels, *Modiolus demissus*; also many oysters are found on muddy bottom.

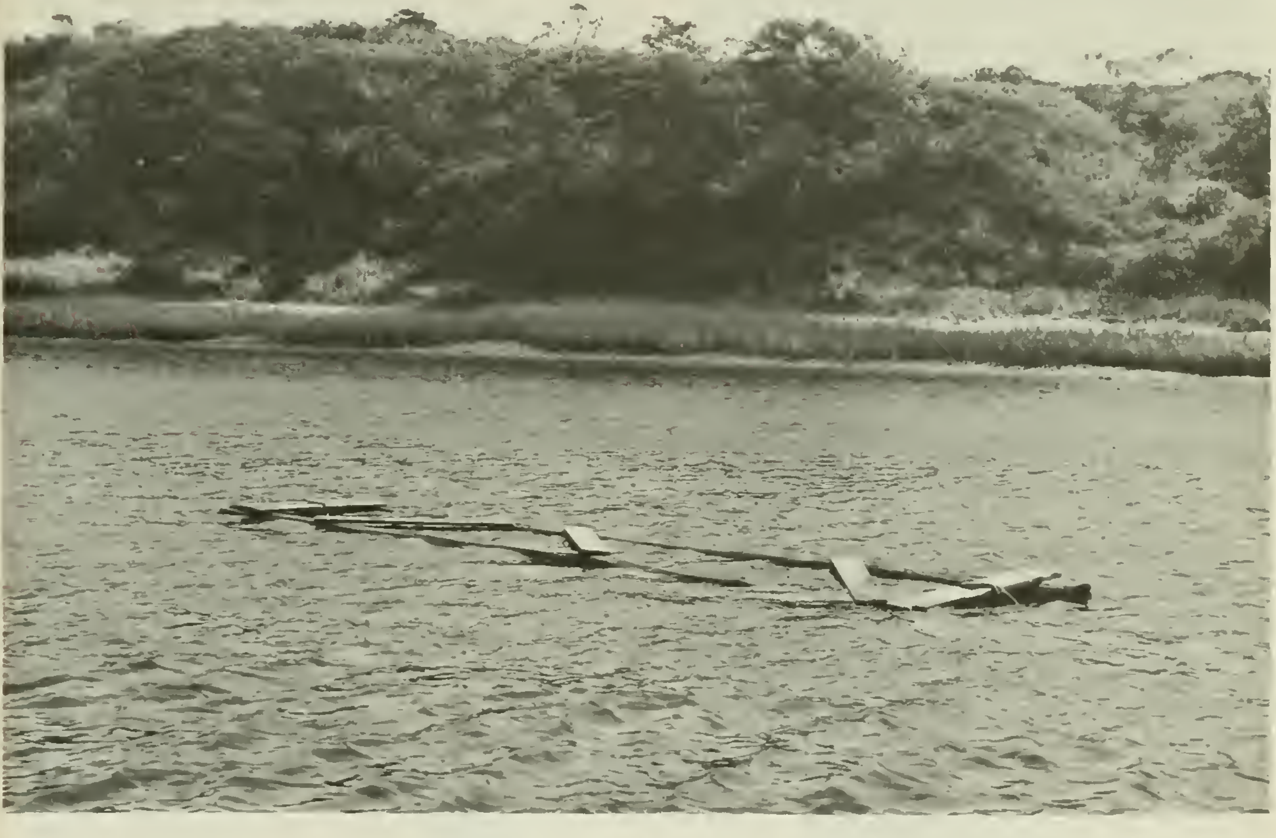

FIGURE 5.—Raft used in the study.

MATERIALS AND METHODS

CONSTRUCTION OF RAFT

The raft (fig. 5) used in the work was constructed of 25-foot cedar logs joined together by wooden crossbars which held it together and kept the logs sufficiently apart to permit free circulation of water. Logs were selected as floats because they were readily available and inexpensive. Each log was floated in the water and notched on the top with an axe. A row of 46 staples (3 inches apart) was placed along the side of each log at right angles to the notches. The log was copper-painted for protection against various fouling and wood-boring organisms. In 1956 the raft consisted of two logs; two more were added in 1957. After storm-damage on January 7, 1958, the raft was reduced to the original two logs.

The raft was moored in Oyster Pond River from September through November 1956, and from April through November 1957 and 1958. During the winters of 1956 and 1957, it was moved and anchored in Oyster Pond to protect it from being damaged and carried away by floating ice which occurs in the river during this period. In November 1958 the raft was dismantled.[2]

ORIGIN OF OYSTERS USED IN THE EXPERIMENT

Oysters used in the 1956 experiment were obtained from a setting that took place during the last week of August between the outlet of Crooked River and Long Beach Point, Wareham River, Mass. Several bushels of cultch were transferred to Oyster Pond River, strung on galvanized wire, and placed on the raft by October 5. All but two strings of Wareham River oysters were destroyed in the storm of January 1958. The two remaining strings were kept attached to the raft until November 1958, when they were removed and taken to the laboratory for measurement.

The oysters used in the 1957 experiments came from Mill Creek, a tidal outlet of Taylors Pond in West Chatham, Mass., which runs for about one-half mile before emptying into Nantucket Sound. The creek bottom is hard sand changing to soft mud near the banks. Along the length of the creek are several sand bars exposed at low tide. Since 1955 a local oyster grower has been catching oyster spat by placing chicken-wire bags each containing one-half bushel of shells on these bars (fig. 6)[3]. In 1957 setting occurred around July 15. On August 12, samples of these oysters were transferred to Oyster Pond River, and by August 30 all were placed on the raft. Fortunately, only a few strings of oysters were lost in the 1958

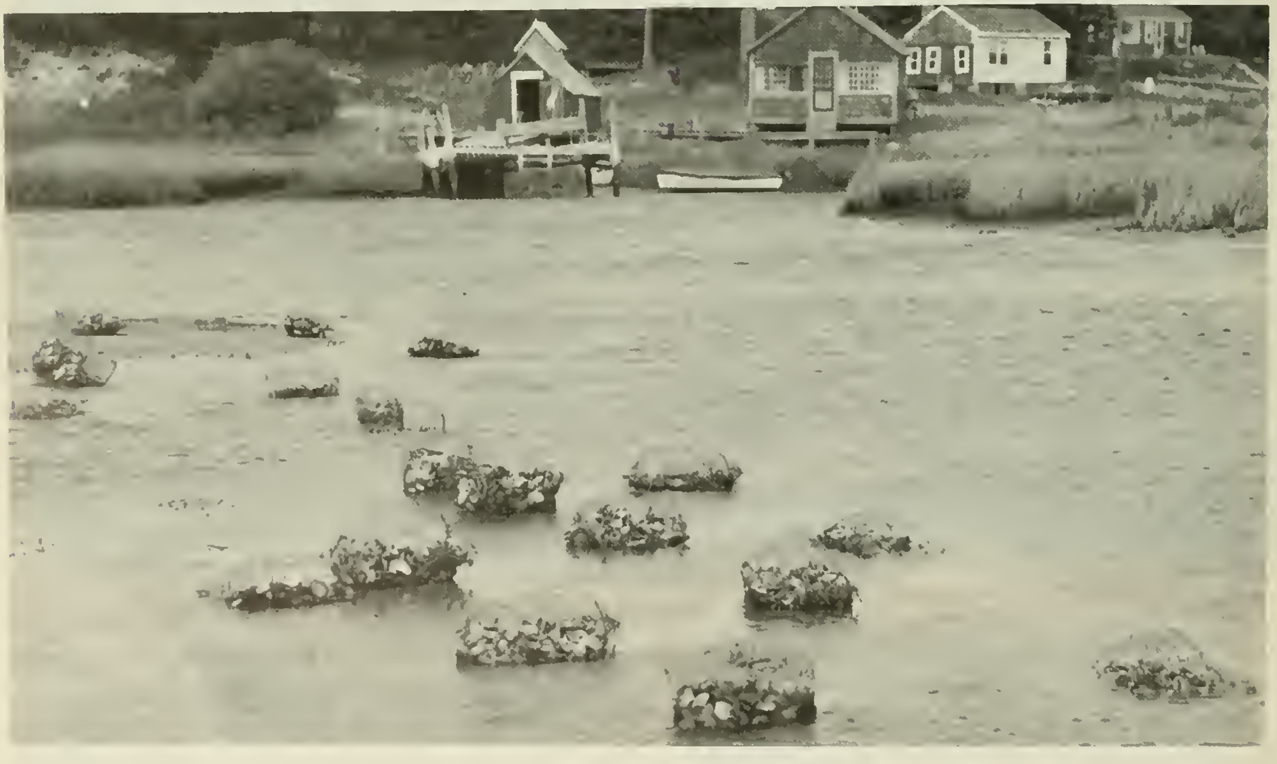

FIGURE 6.—Spat collectors in Mill Creek.

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[2] Shortly after the completion of this study a Fiberglas raft was designed, built, and successfully tested for growing oysters off the bottom. See: Shaw (1960).

[3] Recent studies at Mill Creek indicate that more spat are caught on shells strung on wires and hung horizontally from racks than on shells placed in chicken wire bags.

storm. In November 1958, the Mill Creek oysters were removed from the raft and planted on the bottom. Here they remained until November 1959, when most of them were sold.

ASSEMBLING THE STRINGS OF OYSTERS

To each staple on the log was attached a 5-foot, #14 galvanized wire that had been previously strung with scallop and oyster shells with 5 or more young oysters attached to each. Before stringing the shells, a hole was punched through each one using a tack hammer with a punch brazed to one end (fig. 7). Each string contained approximately 20 pairs of shells, the pairs being separated by a 3-inch piece of plastic tubing. A total of 191 strings were suspended in 1956 and an additional 192 were hung in 1957. After the 1958 storm the total number of strings was reduced to 182.

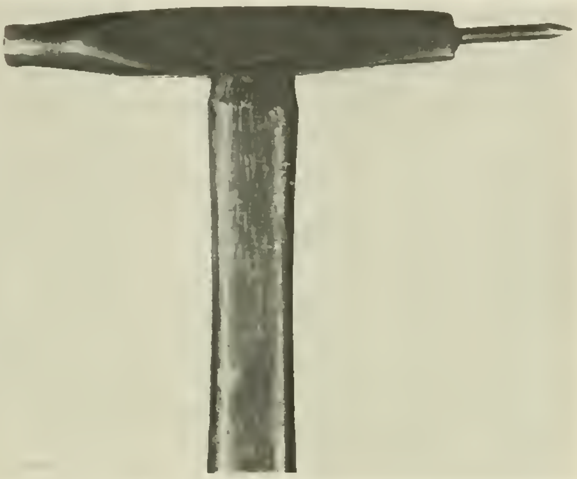

FIGURE 7.—Hammer used to punch holes in shells.

DETERMINING SHELL GROWTH AND OYSTER MORTALITY

Increments of shell growth were noted at monthly intervals. The shell dimensions selected were the height (greatest dorsoventral distance) and length (greatest anteroposterior distance); other measurements such as total volume, total weight, and weight of meat were not taken because the oysters could not be killed during this study without destroying the commercial aspects of the experiment, e.g., the determination of the total number of bushels that can be harvested from a log raft.

The procedure of measuring oysters was as follows: Approximately 100 oysters were taken from both the Wareham River and Mill Creek strings (fig. 8). The oysters were cleaned, taking care not to damage the new shell. They were then measured to the nearest 1.0 mm. with vernier calipers. The same oysters were selected each month in order to keep the cleaning process at a minimum. Immediately after the measurements were completed, the two experimental groups were

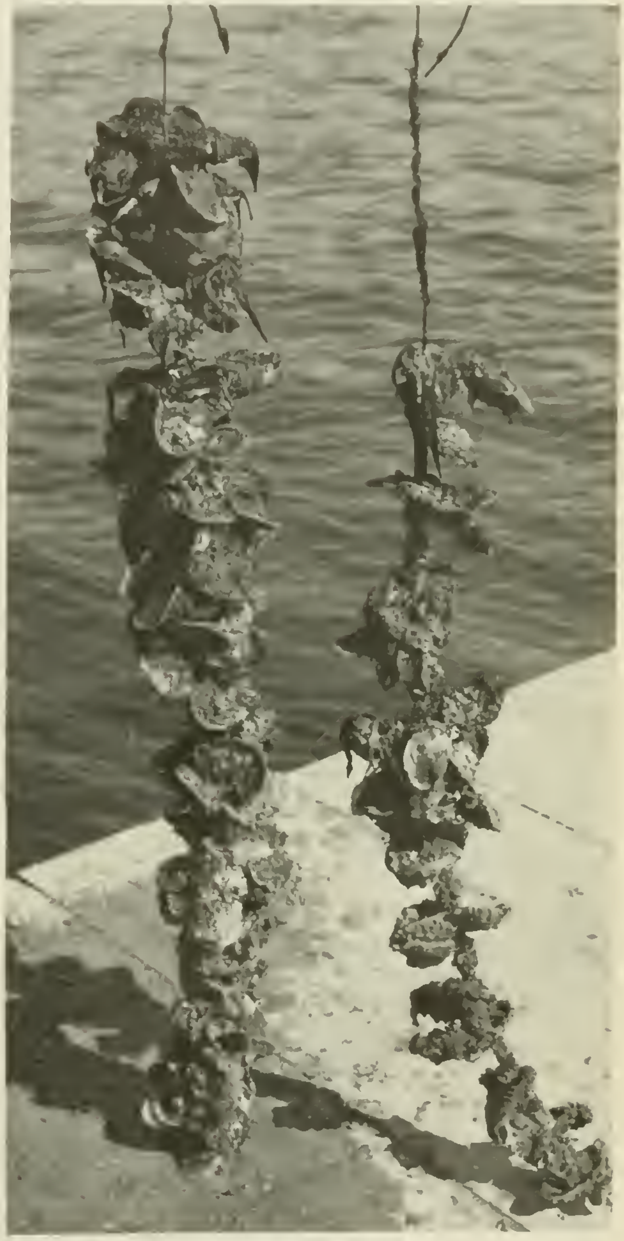

FIGURE 8.—Left, 1957 Mill Creek set grown on log raft for one year. Right, 1956 Wareham River set grown on log raft for two years.

restrung on wires and suspended side by side at a designated spot on the raft.

Just prior to planting the Mill Creek oysters on the bottom, a sample of undisturbed oysters was measured. Their mean height and length were compared with the mean height and length of oysters that had been disturbed and cleaned each month. Little difference between the two groups was found.

In our experiments the shell growth of oysters from Wareham River was observed from the time they were first attached to the raft in the fall of 1956 until the raft was dismantled in 1958. Similar observations of growth were made on oysters from Mill Creek which were attached to the raft in the fall of 1957, then planted on the bottom in the winter of 1958, and finally sold in the winter of 1959. No measurements were taken from mid-November to April because no appreciable shell growth occurred during this period. Oysters on the bottom of the same age and origin as those attached to the raft were measured once each fall. Since these oysters were on private grounds, their disturbance was kept at a minimum.

Monthly survival among the raft oysters was recorded by counting the total number of live oysters on one string. By selecting the same string each month, any decrease in the total number of live oysters from that counted the previous month could be considered natural mortality. A year after the raft oysters were planted on the bottom a random sample was collected and the number of live and dead (left valves only) oysters were counted. The ratio of dead to the total number in the sample was considered natural mortality.

ANALYSIS OF RESULTS

GROWTH

The shell growth rate of the eastern oyster of the Atlantic Coast increases southward and in the Gulf of Mexico. The average height of oysters at the end of the setting year in Connecticut is 19 mm. (Loosanoff, 1946). Moore (1897) found that by the end of the first season of growth oysters of Chesapeake Bay measured 38 mm. in height, whereas in North Carolina this size was reached in 3 months. Moore also observed that 7-month-old South Carolina oysters measured 63 mm. in height. Galtsoff and Luce (1930) working in Georgia, observed 1-year-old oysters ranging from 24 mm. to 69 mm. Ingle (1950) reported that Florida oysters reached 25.4 mm. in 5 weeks, while Butler (1954) found oyster set that grew to 51 mm. in height by the end of the year. The fastest growth was observed in Louisiana where 12-month-old oysters reached 71 mm. in height (Moore and Pope, 1910), although Butler (1954) observed under special conditions at Pensacola (Fla.), a growth of 76 to 101 mm. in 12 months.

Our study shows that the growth of raft oysters from Wareham River was fairly similar to that observed by Loosanoff (1946) for the oysters grown off the bottom at Milford Harbor (Conn.); the mean height in successive years of 11, 49, and 72 mm. for the former compared to 19, 59, and 78 mm. for the latter (table 1). In contrast, the raft oysters from Mill Creek grew faster; the mean height was 28, 67, and 88 mm.

The difference in growth of our Wareham River and Mill Creek oysters was caused by the time of setting of the oysters. Setting in Mill Creek occurred in the middle of July 1957, and by November, when growth stopped, the mean height of these oysters was 28 mm. (table 1, fig. 9). Setting in Wareham River did not take place until late August 1956, and the oysters averaged only 11 mm. in height when growth stopped in November. After the setting year [4] shell growth of both groups was about the same. The total annual increment

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[4] From time of setting to January 1 is the setting year; from January 1 to January 1 is the first year, etc.

TABLE 1.—*Measured mean height and length (mm.), and number of oysters from Wareham River, Long Island Sound, and Mill Creek at the end of growing periods*

[H=height; L=length; N=number]

Time of measurements	Wareham River stock (Grown off bottom in Oyster Pond River)				Long Island stock [1] (Grown off bottom in Milford Harbor)				Mill Creek stock [2] (Grown off bottom in Oyster Pond River)			
	Age	H	L	N	Age	H	L	N	Age	H	L	N
End of setting year	0	11	9	229	0	19	14	--------	0	28	24	105
End of first year	1	49	37	101	1	59	45	--------	1	67	48	103
End of second year	2	72	52	66	2	78	58	--------	2	88	56	50

[1] The information taken from: Loosanoff, Victor L., 1946, Growth of oysters of different ages in Milford Harbor. Proc. Nat. Shellfish Assoc., 1946, pp. 12-21.

[2] At the end of the first year the Mill Creek stock was planted on the bottom.

in mean height for the raft-grown Wareham River oysters at the end of the first and second year was 38 mm., and 23 mm., respectively, compared to 39 mm., and 21 mm. for the raft-grown Mill Creek oysters (fig. 9). From these observations it appears that the Mill Creek oysters do not grow faster, but had an earlier start.

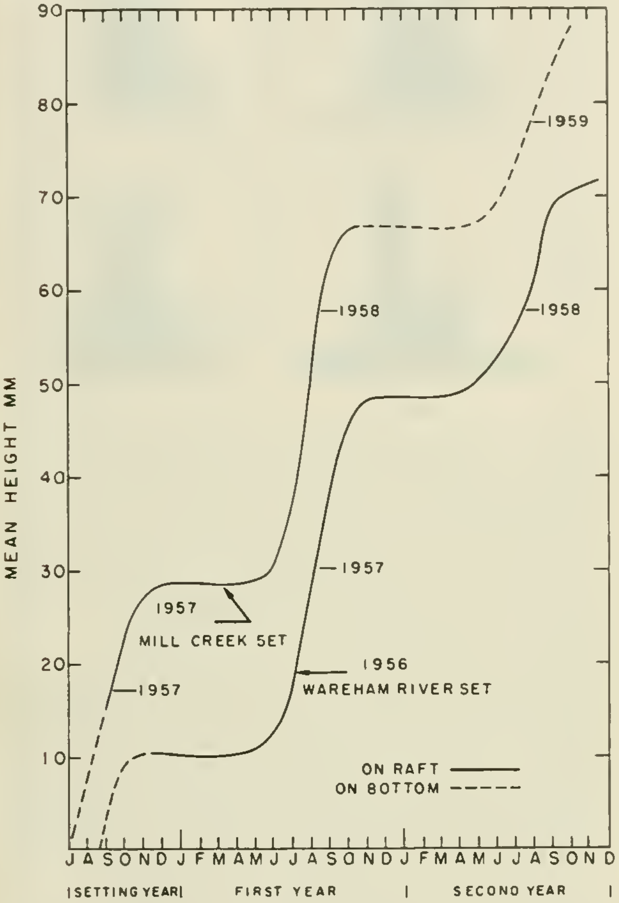

FIGURE 9.—Growth curves of raft-grown Wareham River and Mill Creek oysters.

Because of rapid growth of the oysters attached to the raft, their shells were thin and fragile; the average thickness along the principal axis of the right valve was only 1.4 mm. On November 13, 1958, the raft oysters were planted on the bottom in order to let their shells thicken. After a year on the bottom, the shells of these oysters thickened more than threefold, and averaged 4.6 mm., along the principal axis. The thickening of shell on the bottom is apparently the result of a slower rate of growth in height and length, consequently, larger amounts of calcium carbonate are deposited on the existing shell.

Figure 9 shows the growth curve of Mill Creek oysters from 1957 through 1959. By the end of 1959, following 14 months of attachment to the raft and 1 year on the bottom, the oysters averaged 88 mm., or 3½ inches in height. Market-size for oysters in Massachusetts is 3 inches or greater; therefore, the Mill Creek oysters had attained market-size in 2½ years instead of 4 to 5 years, which elapse when oysters are grown on the bottom in Cape Cod waters.

An actual comparison of raft-grown and bottom-grown Wareham River oysters was made from September 1956 to November 1958. As shown in figure 10 no difference in growth was observed at the end of 1956. By the end of 1957 the raft oysters measured 49 mm. in mean height, whereas those on the bottom were only 36 mm., a difference of 13 mm. The difference increased to 20 mm. by the end of 1958, the raft oysters measuring 72 mm. in height, and the bottom oysters 52 mm. It is of interest to note (fig. 10) that the bottom-grown oysters at the end of 2½ years averaged only 3 mm. larger than the size obtained by the raft oysters in 1½ years.

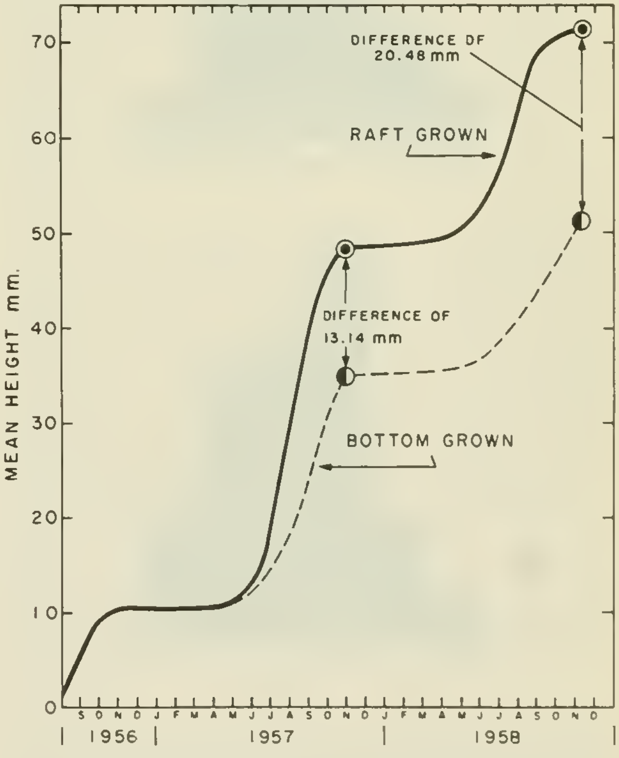

FIGURE 10.—Growth curves of raft-grown and bottom-grown Wareham River oysters. Symbols indicate when shell growth stopped for the year.

In 1957, 76.7, and 82.7 percent of the annual increment in height and length of raft-grown Wareham River oysters occurred during the months of July, August, and September; whereas in 1958, 77.7 and 84.3 percent of the annual growth in height and length occurred during the months of June, July, and August (figs. 11 and 12). For the raft-grown oysters from Mill Creek, 83.7 and 90.4 percentage of the annual increment in height and length occurred during the months of June, July, and August, 1958 (fig. 12).

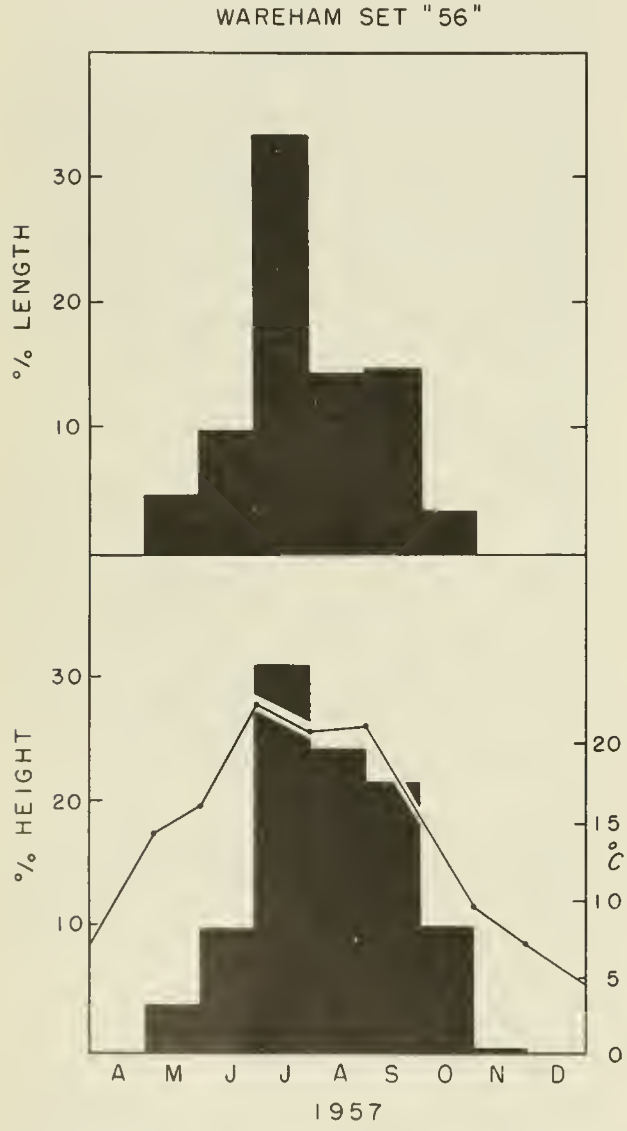

Figure 11.—Monthly increase in height and length of oysters as percentage of total growth during 1957. Temperature curve based on records taken at time of measurement.

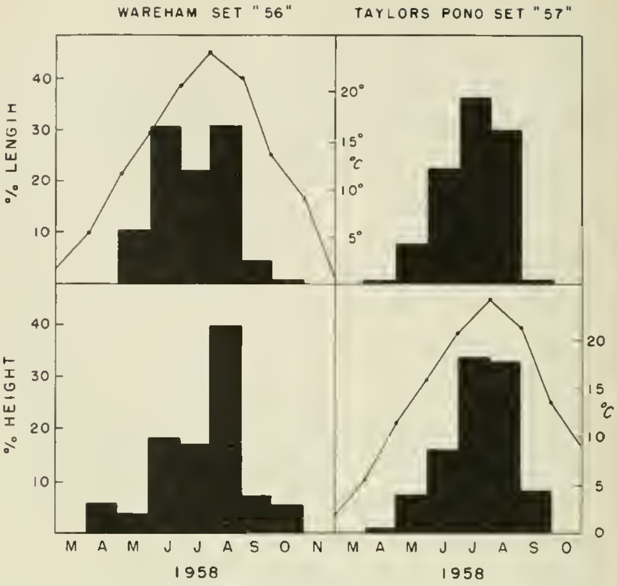

Figure 12.—Monthly increase in height and length of oysters as percentage of total growth during 1958. Temperature curve based on records taken at time of measurement.

EFFECTS OF TEMPERATURE, FOULING, AND SPAWNING ON GROWTH

Temperature

Shell growth did not occur when the water temperature was below 10° C. This observation is in agreement with the findings of Loosanoff and Nomejko (1949) and Walne (1958). In general the oysters in Oyster Pond River grew from April to October inclusive (figs. 11 and 12). During the years 1957 and 1958, approximately 20 percent of the total annual growth occurred when the water temperature was between 10° C. and 15° C., but more than 75 percent of the year's growth took place when the water temperature was above 15° C.

Fouling

The question arose whether the monthly removal of fouling organisms has any effect on the shell growth. On November 17, 1958, the heights and lengths of oysters from two strings were compared; one sample was selected from a string that had remained undisturbed, while the other sample was selected from the string that had been cleaned of fouling animals and plants each month. The results of this comparison are as follows: the average height and length of oysters on the undisturbed string were 65.9 mm. and 48.9 mm., respectively; whereas the clean oysters were 68.6 mm. in height and 47.5 mm. in length. Since little difference was found between the two groups it appears that periodic removal of fouling material had no apparent effect on shell growth.

A year after the oysters were planted on the bottom a sample was collected to determine the extent of fouling. The oyster shells were almost barren of fouling organisms except for some colonies of *Microciona prolifera* and *Didemnum* sp., some Bryozoans, and algae. Most of the original fouling plants and animals had either died or been sloughed off. Noticeably absent was the algae *Gracilaria conferroides* which in other years was one of the principal fouling organisms on the bottom grown oysters.

Spawning

Observations by Loosanoff and Nomejko (1949) and Walne (1958) have shown that the growth of the Eastern oyster in Long Island Sound and the European oyster, *Ostrea edulis*, is not interrupted during the spawning season. In the years 1957 and 1958 the raft oysters were ripe during July. Examination made by the end of August showed that the majority of them had spawned although the actual act of spawning was not observed. Since nearly 60 percent of the total annual shell increment occurred during July and August (see: figs. 11 and 12), it is apparent that shell growth was not inhibited during this period.

MORTALITY OF RAFT OYSTERS

The greatest losses among the suspended oysters occurred when the raft was blown ashore during a winter storm in the early part of 1958. As mentioned, all but two strings of the Wareham River oysters were destroyed, although we were able to save almost all of the strings that contained Mill Creek oysters. In 1958, the mortality among the remaining Mill Creek oysters was determined. By the end of the year 17.7 percent were dead. The number of monthly deaths on one string was recorded from April to December 1958. The deaths per month ranged from 0 to 4 oysters, a total of 14 of the original 79 oysters (table 2). Since there is no known disease in these waters, it is unlikely that the deaths were the result of an epizootic.

TABLE 2.—*Cumulative deaths on one string of raft oysters from April to December, 1958*

Date	Number on one string	Monthly deaths	Sum of dead	Percentage dead
April 17	79	0	------	------
May 2	79	0	------	------
June 2	78	1	1	1.3
July 3	75	3	4	5.1
August 5	74	1	5	6.3
September 5	70	4	9	11.4
October 3	70	0	9	11.4
November 5	66	4	13	16.5
December 2	65	1	14	17.7

In the winter of 1958 the raft-grown oysters were transplanted on the bottom. A sample was collected a year later to determine the mortality that had occurred since planting. Of 87 oysters examined, 64 were alive and 23 were dead, an annual mortality rate of 26.4 percent. The total natural mortality rate for the years 1958 and 1959 was 39.4 percent.[5]

The mortality rate after two years is much greater when oysters are kept on bottom all the time. From a planting of 400 bushels of seed oysters, by a local fisherman in 1956, approximately 90 percent were dead by the fall of 1958. The poor survival of bottom grown oysters is believed to result from losses inflicted by predatory whelks and drills, which invade the oyster beds in large numbers. It appears that by suspending oysters from a raft for one year the number surviving is increased sixfold.

PRACTICAL ASPECTS OF RAFT CULTURE

One of the purposes of this experiment was to determine the commercial feasibility of raft culture in Cape Cod waters. The total cost of materials and labor to construct the 2-log raft, to prepare and attach the strings, and finally to market the oysters was estimated at $248 (p. 492). After one year on the raft and one year on the bottom 25 bushels of raft-grown oysters (averaging 250 to a bushel) were sold and 7 bushels were replanted. The wholesale value of these 32 bushels in 1959 at the Chatham price of $11.50 a bushel was $368, yielding a gross profit of $120 or $3.75 a bushel for this small-scale operation.

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[5] Based on a progressive death rate; if there are 1,000 oysters and 17.7 percent die in the first year, 823 oysters are still alive. If 26.4 percent of the remaining oysters die during the second year, there are still 606 of the original 1,000 oysters alive, or a mortality rate for the two years of 39.4 percent.

A summary of the total cost of material and labor to construct a 2-log raft, to prepare the strings, and to market oysters follows:

Materials:	
Two 25-foot cedar logs	$30.00
Polyethylene tubing used for spacers ($23.75/1,000 feet)	16.00
Copper paint ($7.75/gallon)	15.50
Two 50-pound mud anchors ($18.50/anchor)	37.00
Miscellaneous (rope, peavie, staples)	10.00
Commercial spat ($1.50/bushel)	30.00
Total costs for material	$138.50

Labor: (Chatham $1.50 hourly wage)	
2 hours, cut and straighten wire	$3.00
8 hours, cut polyethylene tubing	12.00
4 hours, paint and staple logs	6.00
36 hours, assort, put in holes, and string shells	54.00
3 hours to moor raft and secure strings	4.50
4 hours to disassemble raft and plant oysters	6.00
16 hours to tong, cull, and pack oysters	24.00
Total costs for labor	109.50
Grand total (materials and labor)	$248.00

In 1959, the oystermen at Chatham were paying as much as $7 a bushel for Long Island oysters. These oysters were planted in the spring to grow and fatten during the summer, and were sold in the fall at $11.50 a bushel, with a gross profit of $4.50 a bushel. Approximately the same number of bushels of oysters planted are sold because natural mortality balances any increase in volume resulting from shell growth. The net profit is less because the labor costs, to plant, gather, and pack the oysters for market, are not known [6] and have not been deducted.

One cannot overlook the fact that the oystermen at Chatham are earning $4.50 a bushel each year, whereas the profit of $3.75 a bushel earned from raft-grown oysters require 2 years. Profits from raft culture could be earned on a yearly basis by suspending new strings of young oysters at the time when the 1-year-old raft-grown oysters are planted on the bottom, thus developing a continuous operation.

The cost of materials in raft oyster culture may be considerably reduced and the profit increased if the operation were conducted on a large and continuous scale.

DISCUSSION AND RECOMMENDATIONS

Our data show that raft-grown oysters grow faster and have a higher survival rate than those kept all the time on bottom. The question arises whether this faster growth and higher survival is enough to warrant the extra cost for materials and labor necessary for raft culture. From the findings of these preliminary observations it appears that raft-grown oyster farming may be feasible in Cape Cod waters. The study should now be repeated on a larger semicommercial scale. A pilot oyster farm should be tried to ascertain the true commercial practicability of raft-grown oysters in Massachusetts.

The raft used in our study was primitive and could only support the weight of 32 bushels of oysters. By increasing its buoyancy more oysters could be attached and the yield would, therefore, be greater.

Oyster Pond River was selected as the site for this study because the area was easily accessible by road. Though it proved a satisfactory site for our experiments, this river is not suitable for raft oyster culture on a commercial scale. Because the river is shallow, only 5-foot strings could be used. In deeper water longer strings could be attached and the yield would increase considerably. The danger of floating ice in the winter also makes the river undesirable for raft culture.

There are many salt-water ponds along the shore of Cape Cod were raft culture could be established. For example, Taylors Pond, West Chatham (Mass.) appears suitable for this purpose. Here the water is more than 9 feet in depth and there is little danger of floating ice. Additional research is necessary to locate the ponds on the Cape that are suitable for raft culture, and to determine their productive capacity.

The importance of suspending an early set should not be overlooked, if and when raft oyster culture is conducted on a commercial scale. Our observations show that marketable oysters are obtained in 2½ years when a July set is attached to the raft. On the other hand, when an August set is suspended the average oyster after 2½ years is less than the 3-inch legal minimum size. It would be necessary to carry these oysters for another season. Losses inflicted by predators during this time would reduce profits considerably.

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[6] Oystermen working in oyster Pond River rarely employ hired labor.

The development of raft culture in Cape Cod waters would not eliminate the need for suitable planting grounds. As mentioned earlier the shells of the raft oysters are thin and fragile because their growth is rapid. It is, therefore, necessary to plant them on the bottom to thicken their shells. Since most oysters grown in Massachusetts are purchased to be served on the half-shell, restaurants and fish markets require an oyster with a reasonably thick shell. From our obsevations, it appears that such an oyster can be obtained by planting the raft-grown oysters on the bottom for one year.

It should not be forgotten that the oystermen of Cape Cod are almost entirely dependent on out-of-State bedding stock. With the present decline of oysters more and more Bay State growers are going out of business. To date the seed resources of Massachusetts are not being utilized. By developing the setting areas, the oyster industry of the State could become self-sustaining and independent of out-of-State bedding stock. The introduction of raft culture in local waters would be one way of utilizing the State's seed resources.

In conclusion, it must be realized that the study was conducted in Cape Cod waters where more than 75 percent of the annual increment of shell-growth occurs during three summer months and where no growth takes place during the winter. Other areas might give different results, especially in the South where shell growth is not interrupted by hibernation. It would be of interest to repeat the raft experiments in the more southern waters.

SUMMARY

1. The harvest of oysters in Massachusetts has dropped 83.3 percent in the last 50 years. In 1958, only 113 thousand pounds of oyster meats where havested, an all-time low for the State.

2. The objective of the experiment was to determine whether raft oyster culture is commercially feasible in Cape Cod waters.

3. A log raft was moored in Oyster Pond in the winter and in Oyster Pond River during the summer. Atttached to the logs were wire strings containing shells with oysters from Wareham River and Mill Creek. The mean height for raft oysters in successive years was as follows: Wareham River stock, 11, 49, 72 mm.: Mill Creek stock, 29, 67, and 88 mm.

4. Oysters attached to the raft had a faster growth rate than those on the bottom; by the end of the first year the raft-grown oysters from Wareham River were 13 mm. greater in mean height than those growing on the bottom. The difference increased to 20 mm. by the end of the second year.

5. No measurable shell growth was observed when the water temperature was below 10° C. Seventy-five percent of the year's growth took place when the water temperature was above 15° C.

6. Greatest shell growth occurred when the oysters were in spawning condition.

7. Both fouled and cleaned oysters had the same growth rates.

8. Survival of raft oysters was about 6 times greater than for oysters growing on the bottom. The high losses of bottom oysters is believed to be due to predation by whelks and drills.

9. The experiment demonstrated that oysters can be grown from seed to market-size in 2½ years. Wild oysters take from 4 to 5 years to reach market-size in Cape Cod waters.

10. Thirty-two bushels of raft-grown oysters were harvested. Of these, 25 bushels were sold and 7 bushels were replanted. A gross profit of $120 or $3.75 a bushel was earned from the two-log raft. It is likely that costs for materials and labor would be reduced and profits correspondingly increased if raft culture were conducted on a larger scale.

11. The development of raft oyster culture in Cape Cod waters appears to be commercially feasible. It is recommended that raft culture on a larger scale be conducted for the purpose of ascertaining the true commercial value of this method.

LITERATURE CITED

ABBOTT, R. TUCKER.
1954. American seashells. D. van Nonstrand Co., Princeton, N.J., 541 p.

BELDING, DAVID L.
1909. A report upon the mollusk fisheries of Massachusetts. Wright and Potter Printing Co., Boston, Mass., 243 p.

BONNOT, PAUL.
1935. The California oyster industry. California Fish and Game, vol. 21, No. 1, p. 65–80.

BUTLER, PHILIP A.
1954. Summary of our knowledge of the oyster in the Gulf of Mexico. U.S. Fish and Wildlife Service, Fishery Bulletin, No. 89, vol. 59, p. 479–489.

Galtsoff, Paul S.
1956. Ecological changes affecting the productivity of oyster grounds. Transactions of the 21st North American Wildlife Conference, p 409–419.

Galtsoff, Paul S., and R. H. Luce.
1930. Oyster investigations in Georgia. U.S. Bureau of Fisheries, Document 1077, Appendix V to the Report of the Commissioner of Fisheries for the fiscal year 1930, p. 61–100.

Galtsoff, Paul S., H. F. Prytherch, and H. C. McMillin.
1930. An experimental study in production and collection of seed oysters. U.S. Fish and Wildlife Service, Document 1088, Fishery Bulletin, vol. 46, p. 197–263.

Ingersoll, Ernest.
1881. A report on the oyster-industry of the United States. Section 10 (monograph B). *In* The history and present condition of the fishery industries. Tenth census of the U.S., Department of the Interior. Washington, D.C., 251 p.

Ingle, Robert M.
1950. Summer growth of the American oyster in Florida waters. Science, vol. 112, No. 2908, p. 338–339.

Kesteven, G. L.
1947. Biology and cultivation of oysters. Fisheries Newsletter, vol. 6, No. 3, p. 4–5, 16.

Loosanoff, Victor L.
1946. Growth of oysters of different ages in Milford Harbor. National Shellfisheries Association Convention Addresses, 1946, p. 12–21.

Loosanoff, Victor L., and Charles A. Nomeyko.
1949. Growth of oysters, *O. virginica*, during different months. Biological Bulletin, vol. 97, No. 1, p. 82–94.

Moore, H. F.
1897. Oysters and methods of oyster culture. U.S. Commission of Fish and Fisheries, Report of the Commissioner for 1897, (vol. 23), p. 263–340.

Moore, H. F. and T. E. Pope.
1910. Oyster culture experiments and investigations in Louisiana. U.S. Bureau of Fisheries, Document 731, Report of the Commissioner for 1908, 52 p.

Quayle, D. B.
1956. The raft culture of the Pacific oysters in British Columbia. Fisheries Research Board of Canada, Progress Reports of the Pacific Coast Stations, No. 107, p. 7–10.

Shaw, William N.
1960. A fiberglas raft for growing oysters off the bottom. The Progressive Fish-Culturist, vol. 22, No. 4, p. 154.

Wallace, David H.
1959. Japanese oyster culture. Oyster Institute of North America, Special Report No. 2, 4 p.

Walne, Peter R.
1958. Growth of oysters (*Ostrea edulis L.*). Journal of the Marine Biological Association of the United Kingdom, vol. 37, No. 3, p. 591–602.

APPENDIX A

Mean height and length, standard deviation, and standard error of the mean for raft-grown oysters

Table A–1.—*1956 Wareham River oysters*

Date sampled	Mean height (mm.)	Standard deviation (mm.)	Standard error	Mean length (mm.)	Standard deviation (mm.)	Standard error	*N*
1956							
Oct. 11	9.9	3.6	.31	8.4	3.4	.28	140
Oct. 25	10.3	3.4	.23	9.0	3.5	.23	231
Nov. 8	10.4	3.6	.24	9.1	3.1	.21	229
Dec. 4	10.5	3.6	.23	9.0	3.1	.21	229
1957							
April 12	10.8	3.5	.35	9.5	3.2	.32	99
April 26	10.7	3.5	.33	9.0	3.2	.31	110
May 9	12.7	4.1	.39	10.9	3.6	.34	110
May 16	12.4	4.4	.39	10.4	3.9	.34	129
May 29	12.1	4.0	.35	10.2	3.8	.33	134
June 27	15.7	6.3	.57	13.0	5.6	.51	120
July 29	27.5	6.3	.61	22.7	5.6	.54	109
Aug. 29	36.6	6.9	.70	29.6	6.1	.62	97
Sept. 27	44.9	7.6	.78	36.8	6.8	.70	95
Oct. 29	48.7	8.0	.79	37.8	6.6	.65	102
Nov. 29	48.8	8.0	.80	37.1	6.8	.68	101
1958							
April 17	49.9	9.3	1.05	35.5	6.9	.78	79
May 2	51.1	9.0	1.02	34.9	7.1	.80	79
June 2	52.0	9.3	1.05	36.7	7.0	.79	78
July 3	56.0	9.4	1.09	41.9	7.5	.87	75
Aug. 5	59.9	9.2	1.07	45.8	7.7	.90	74
Sept. 5	69.1	11.7	1.40	51.2	8.9	1.06	70
Oct. 3	70.7	10.8	1.29	52.0	8.9	1.06	70
Nov. 5	71.9	10.6	1.31	52.1	7.7	.95	66

Table A–2.—*1957 Milt Creek oysters*

Date sampled	Mean height (mm.)	Standard deviation (mm.)	Standard error	Mean length (mm.)	Standard deviation (mm.)	Standard error	*N*
1957							
Aug. 29	15.2	6.8	.67	13.7	5.8	.57	103
Sept. 27	23.1	8.0	.73	20.6	6.8	.62	120
Oct. 29	27.5	7.8	.76	23.0	6.5	.63	110
Nov. 29	28.5	8.0	.80	23.6	6.8	.68	105
1958							
Apr. 17	27.3	7.6	.75	21.6	6.2	.62	102
May 2	27.5	7.6	.75	21.7	6.5	.64	103
June 2	30.4	7.4	.66	23.9	6.2	.56	124
July 3	36.7	8.9	.86	30.1	7.7	.74	108
Aug. 5	50.3	8.9	.88	39.9	7.7	.77	102
Sept. 5	63.4	11.1	1.09	48.1	8.3	.82	103
Oct. 3	66.7	11.9	1.17	48.4	8.8	.86	104
Nov. 5	66.6	11.4	1.12	48.2	8.5	.83	103
1959							
Oct. 6	88.5	12.0	1.70	56.5	6.8	.95	50

APPENDIX B

Total monthly growth and percentage of growth, 1957–58

TABLE B–1.—*Wareham River oysters*

Date sampled	Mean height (mm.)	Monthly growth (mm.)	Monthly growth in percentage of total increment during year (mm.)	Mean length (mm.)	Monthly growth (mm.)	Monthly growth in percentage of total increment during year (mm.)	*N*
1957							
Apr. 26	10.7	----------	----------	9.0	----------	----------	110
May 29	12.1	1.4	3.7	10.2	1.2	4.1	134
June 27	15.7	3.6	9.4	13.0	2.8	9.7	120
July 29	27.5	11.8	31.0	22.7	9.7	33.7	109
Aug. 29	36.6	9.1	23.9	29.6	6.9	24.0	97
Sept. 27	44.9	8.3	21.8	36.8	7.2	25.0	95
Oct. 29	48.7	3.8	9.9	37.8	1.0	3.5	102
Nov. 29	48.8	0.1	0.3	37.1	----------	----------	101
1958							
Apr. 17	49.9	----------	----------	[1] 35.5	----------	----------	79
May 2	51.1	1.2	5.5	34.9	----------	----------	79
June 2	52.0	0.9	4.1	36.7	1.8	10.4	78
July 3	56.0	4.0	18.2	41.9	5.2	30.2	75
Aug. 5	59.9	3.9	17.7	45.8	3.9	22.7	74
Sept. 5	69.1	9.2	41.8	51.2	5.4	31.4	70
Oct. 3	70.7	1.6	7.3	52.0	0.8	4.7	70
Nov. 5	71.9	1.2	5.4	52.1	0.1	0.6	66

[1] Original sample measured in 1957 was lost in a winter storm.

TABLE B–2.—*Mill Creek oysters*

Date sampled	Mean height (mm.)	Monthly growth (mm.)	Monthly growth in percentage of total increment during year (mm.)	Mean length (mm.)	Monthly growth (mm.)	Monthly growth in percentage of total increment during year (mm.)	*N*
1958							
Apr. 17	27.3	----------	----------	21.6	----------	----------	102
May 2	27.5	0.2	0.5	21.7	0.1	0.4	103
June 2	30.4	2.9	7.4	23.9	2.2	8.2	124
July 3	36.7	6.3	16.0	30.1	6.2	23.1	108
Aug. 5	50.3	13.6	34.5	39.9	9.8	36.6	102
Sept. 5	63.4	13.1	33.2	48.1	8.2	30.6	103
Oct. 3	66.7	3.3	8.1	48.4	0.3	1.1	104
Nov. 5	66.6	----------	----------	48.2	----------	----------	103

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